2006

Predation On The Eastern Oyster Crassostrea Virginica On Intertidal Reefs Affected By Recreational Boating

Jennifer Stiner
University of Central Florida

PREDATION ON THE EASTERN OYSTER *CRASSOSTREA VIRGINICA* ON INTERTIDAL REEFS AFFECTED BY RECREATIONAL BOATING

by

JENNIFER LORRAINE STINER
B.S. Erskine College, 2003

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Arts and Sciences
at the University of Central Florida
Orlando, FL

Spring Term
2006

ABSTRACT

Widely regarded as a keystone species and ecosystem engineer, the eastern oyster *Crassostrea virginica* plays a vital role in estuarine environments. Complex, three-dimensional oyster reefs act as havens for biodiversity and contribute to ecological processes. Recently, concern for this resource has arisen in Mosquito Lagoon, Florida, the southernmost limit along the Atlantic coast for undisturbed, intertidal reefs of *C. virginica*. Since the 1990s, intense recreational boating activity has caused atypical dead margins (mounds of disarticulated shells) to emerge on the seaward edges of oyster reefs located along major navigational channels. Once dead margins are formed, little is known about their influence on biotic composition and interactions on oyster reefs. This study focused on the affect of dead margins on: (1) mobile species biodiversity and distribution, (2) reef architecture, and (3) the affect of structural variables on predation of juvenile oysters.

To determine if dead margins influenced the biodiversity of mobile species on oyster reefs, lift nets (1 m^2) were deployed within Mosquito Lagoon for one year (June 2004 - June 2005). These nets (5/site) were deployed on the back-reef areas of six reefs (3 reference reefs and 3 reefs containing dead margins). To simulate reef habitat, one and a half liters of live oysters were placed within each net. Lift nets were checked monthly and surveyed for all mobile species. The resulting data were assimilated into a species inventory containing 65 species of fishes, mollusks, crustaceans, worms, and echinoderms. The two most abundant species present on reefs in Mosquito Lagoon were the big-claw snapping shrimp *Alpheus heterochaelis*, a filter-feeder, and the flat-back mud crab *Eurypanopeus herbstii*, a predator of oyster spat. Contrary to expections, analyses of community metrics showed that dead margins did not significantly affect the biodiversity of back-reef areas on oyster reefs.

Modified lift nets (0.25 m^2) were placed on six different oyster reefs (3 reference reefs and 3 containing dead margins) to test if dead margins affected the distribution of mobile species inhabiting oyster reefs. Nine nets were arranged to cover three separate areas of each reef: the fore-reef (3 nets), mid-reef (3 nets), and back-reef (3 nets). Half a liter of oyster shells were placed inside each net. These nets were checked weekly, for five weeks and species richness, density, and biomass were recorded. Analyses revealed that all community metrics were significantly higher on reference reefs than reefs affected with dead margins. Further, a significant drop in all three metrics was seen on the mid-reef area of affected reefs. The absence of species on this area is hypothesized to be due to a lack of water, shade, and habitat complexity.

To document architectural differences, two types of transects were run along five reference reefs and five reefs with dead margins. First, quadrat transects determined the percent of live oysters, the percent of shell clusters, topographic complexity (using chain links), and the angle of shells on each reef type. Transect lines were stretched parallel to the water line and covered all three reef areas (fore-reef, mid-reef, and back-reef). The results showed reference reefs to have approximately four-fold more live oysters, approximately twice as many shell clusters, and significantly greater topographic complexity. Numbers of live oysters and shell clusters were greater on the fore-reef and back-reef areas of both reef types.

Second, laser transects were used to record reef profiles and the slope of fore-reef areas. Transect lines were stretched perpendicular to the water line and every 20 cm the distance between the lagoon bottom and reef top was measured. Vertical reef profiles and fore-reef slopes were significantly different between reference reefs and reefs with dead margins. Dead margins compressed reef widths, increased center peaks, and increased slopes on the fore-reef area by two-fold.

Lastly, field experiments were conducted to determine the affect of dead margins on the vulnerability of oyster spat to predation. Structural variables (e.g. shell orientation, single versus shell clusters, reef slope) were manipulated and effects on oyster mortality were observed. Three predators were tested: the blue crab *Callinectes sapidus*, the common mud crab *Panopeus herbstii*, and the Atlantic oyster drill *Urosalpinx cinerea*. Structural variables did not have a significant influence on oyster mortality; however, a significant difference was established between predators. *Panopeus herbstii* consumed the most juvenile oysters, followed by *U. cinerea* and then *C. sapidus*.

Together, these findings document ecological implications of dead margins on *C. virginica* reefs and reinforce the urgent need for enhanced regulations and restoration. If the intensity of recreational boating remains unregulated, dead margins will continue to increase. Thus, in order to maintain the diversity and productivity of Mosquito Lagoon, it is crucial to fully understand how dead margins alter the biogenic habitat and biotic communities of oyster reefs.

ACKNOWLEDGMENTS

Funding was provided by the Aylesworth Foundation (Florida Sea Grant), the University of Central Florida Biology Department, including a Research Enhancement Award, and Florida Sea Grant (Dr. Linda Walters). I thank the University of Central Florida and Canaveral National Seashore for their support in this research. I also thank my thesis advisor, Dr. Linda Walters, and my committee members Dr. Reed Noss and Lori Morris (St. Johns River Water Management District). I greatly appreciate everyone who helped with data collection: A. Barber, S. Bales, M. Bender, M. Black, M. Boudreaux, A. J. Clark, T. Clark, W. Clark, M. Donnelly, P. Gaynon, N. Gillis, C. Glardon, K. Kirby, J. Ledgard, A. McLellan, M. Nikolich, J. Sacks, P. Sacks, A. Simpson, E. Stiner, J. C. Stiner, J. K. Stiner, and J. Wojtkowski. I thank the following for assistance with species identification: Dr. R. Gilmore (gobies), L. Haynes (crustaceans), C. Holden (crustaceans), and E. Reyier (fishes). I also thank P. Quintana-Ascencio for guidance with statistical analyses.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

GENERAL INTRODUCTION

The Indian River Lagoon

The Indian River Lagoon system (IRL) is one of the most important and productive estuarine systems in North America (Tremain and Adams 1995; Walters et al. 2001). Stretching approximately 250 km and covering 40 percent of Florida's east coast, the IRL consists of the Indian River, Banana River, and Mosquito Lagoon (Figure 1) (Walters et al. 2001). It is highly productive, containing one of the highest species diversities of any estuary in North America (Provancha et al. 1992). The IRL supports over 3,000 species of animals and plants (Smithsonian Institute 2001). Both the state of Florida and the Environmental Protection Agency have recognized the ecological importance of this area by designating the IRL as one of Florida's Outstanding Waterways, an Aquatic Preserve, and an Estuary of National Significance (Walters et al. 2001).

The northernmost portion of this system, Mosquito Lagoon, is a bar-built type estuary bordered by Atlantic Coastal Ridge on the west and the Atlantic Beach Ridge on the east. It stretches 60 km and encompasses 60,000 acres (Walters et al. 2001). Almost all of Mosquito Lagoon lies within the boundaries of Canaveral National Seashore (CANA) (Walters et al. 2001). A unique characteristic of the Lagoon is its location along the border between temperate and tropical climates (Figure 1) (Smithsonian Institute 2001). This may contribute to its richness in diversity (Walters et al. 2001). Over the course of a year, species composition varies according to the climate. Tropical species dominate during the summer months while temperate species take over during the winter months (Walters et al. 2001). Overall, Mosquito Lagoon acts as a refuge for 14 federally-listed threatened and endangered species, is nationally recognized for recreational fishing, and is the southernmost limit along the Atlantic coast for undisturbed, intertidal reefs of the eastern oyster *Crassostrea virginica* (Grizzle and Castagna 1995).

Importance of *Crassostrea virginica*

The broad geographic range of *Crassostrea virginica* stretches 8000 km from the Gulf of St. Lawrence in Canada (48º N) down to the coasts of Brazil and Argentina (50º S) (Galstoff 1964; Gosling 2003). Considered a keystone species and ecosystem engineer (Paine 1969; Dame 1996; Breitburg et al. 2000; Coen and Luckenbach 2000), oysters help support hundreds of species. As generations of oysters build upon on one another, structural irregularities and infoldings occur. The increasingly complex structure of an oyster reef offers a variety of microhabitats for estuarine species to inhabit (Sellers and Stanley 1984; Durako et al. 1988; Dame 1996; Kennedy et al. 1996; Eggleston et al. 1999). Surrounded primarily by soft sediments, oysters also provide a hard substrate for epibiotic species in the middle of an otherwise monotonous environment (Wells 1961; Lenihan and Micheli 2001). Along the south Atlantic coast, the number and total densities of fish, invertebrates, and algal species greatly increases in areas containing oyster reefs (Bahr and Lanier 1981). In estuaries in North Carolina, 303 species were found to be associated with oyster reefs (Wells 1961).

Oysters actively contribute to ecological processes within Mosquito Lagoon's estuarine system (Smithsonian Institution 2001). While reefs stabilize the sediment and influence water currents, individuals help improve water quality (Bahr 1976; Bahr and Lanier 1981; Lenihan

1999; Nelson et al. 2004). Oysters feed by filtering water through their gills and straining microalgae and organic matter from the water column (Dame et al. 1984; Newell 1988; Gosling 2003). Oysters filter large quantities of water, up to 1500 times their body volume per hour (Loosanoff and Nomejko 1946). This filtering allows oysters to improve water quality and potentially reduce the affects of contaminants and pollution (Officer et al. 1982; Newell 1988; Lenihan 1999; Nelson et al. 2004).

Threats to oyster reefs and communities in Mosquito Lagoon

Recently, concern has arisen over the viability and survival of oyster reefs located in Mosquito Lagoon. Since 1943, atypical dead margins have begun to emerge on the seaward edges of oyster reefs located along major navigational channels (Figure 2) (Grizzle and Castagna 1995; Grizzle et al. 2002). These dead margins consist of mounds of disarticulated shells that often extend one meter above mean high water (Grizzle et al. 2002). As of 2000, 15% of the oyster reefs within Mosquito Lagoon contained dead margins (Grizzle et al. 2002).

The development of dead margins has been linked to increases in recreational boating (L. Walters unpublished data). Well-known for its beautiful scenery and quality fishing, Mosquito Lagoon has attracted more and more recreational boaters and fishers in recent years (Wall et al. 2005). Between 1998 and 2003, the numbers of registered recreational boats increased 42.8% in counties surrounding Mosquito Lagoon (Harvey 2004; Wall et al. 2005). This has led to increased water motion and sediment re-suspension within the Lagoon (Wall et al. 2005). Reefs containing dead margins are exposed to significantly higher water motion and sediment loads than reefs in reference, unaffected conditions (Wall et al. 2005). Consequentially, the survival of juvenile oysters on reefs containing dead margins have been reduced (Wall et al. 2005).

Although extensive research has been conducted on the causes of dead margins, little is known about their influence on oyster reef communities once they are formed. The goal of my research was to document architectural changes to reef structure and the subsequent affects of dead margins on biotic composition and interactions.

CHAPTER ONE: SPECIES INVENTORY AND COMMUNITY METRICS

Introduction

Widely regarded as a keystone species and ecosystem engineer, the eastern oyster *Crassostrea virginica* plays a vital role in estuarine environments (Jones et al. 1994; Dame 1996). As generations of oysters build upon on one another, structural irregularities and infoldings create complex three-dimensional reef structures. Thus, oyster reefs act as havens for biodiversity, offering a variety of microhabitats for estuarine species to inhabit (e.g. Sellers and Stanley 1984; Dame 1996; Kennedy et al. 1996). Surrounded primarily by soft-sediments, oysters provide a hard substrate for epibiotic invertebrates in the middle of an otherwise unvaried environment (e.g. Wells 1961; Bartol et al. 1999; Micheli and Peterson 1999). Reefs also provide protection from predation and dessication for smaller estuarine species (e.g. Bahr and Lanier 1981; McDonald 1982; Grant and McDonald 1979; Lenihan 1999; Nelson et al. 2004).

Along the south Atlantic coast, the number and total densities of fishes, invertebrates, and algal species greatly increases in areas containing oyster reefs (Arve 1960; Dame 1979; Bahr and Lanier 1981; Crabtree and Dean 1982; Breitburg 1992; Wenner et al. 1996; Coen et al. 1999). In estuaries in North Carolina, 303 species were found to be associated with oyster reefs (Wells 1961). Furthermore, oyster reefs have been recognized as essential fish habitat, providing shelter for fin-fish, mollusks, and crustaceans (USDOC 1997; Coen et al. 1999).

Mosquito Lagoon, Florida is the southernmost limit along the Atlantic coast for undisturbed, intertidal reefs of *C. virginica* (Walters et al. 2001). It is the northernmost portion of the Indian River Lagoon system, one of the most productive and diverse estuaries in North

America (Figure 1) (Tremain and Adams 1995; Walters et al. 2001). Found adjacent to spoil island areas impounded to control for mosquitos, intertidal oyster reefs play a vital role in maintaining biodiversity and productivity of this lagoon system (Walters et al. 2001). However, since 1943, intense recreational boating activity has caused atypical mounds of disarticulated shells (dead margins) to emerge on the seaward edges of oyster reefs located along major navigational channels (Figure 2) (Grizzle and Castagna 1995; Grizzle et al. 2002). As of 2000, 15% of the oyster reefs within Mosquito Lagoon contained dead margins (Grizzle et al. 2002). Concern for the survival of *C. virginica* reefs within Mosquito Lagoon has initiated numerous research and restoration efforts.

To date, no studies have looked at the biological diversity on oyster reefs within Mosquito Lagoon, Florida. This study inventories mobile species associated with these oyster reefs. The results are compared with those from Tolley et al. (2005) and Coen et al. (1999), who created inventories of fishes and decapods for the west coast of Florida and the Atlantic coast of South Carolina, respectively. To determine the affect of dead margins on reef biodiversity and species distributions, comparisons were made between community metrics on reference reefs (i.e. reefs in reference condition) and affected reefs (i.e. reefs that contain dead margins).

Methods: Lift nets

Study site

Within Mosquito Lagoon, the average water depth is 1 m and the current is primarily wind-driven (Walters et al. 2001). Depending on rainfall, salinity ranges between 18 and 45 ppt

(Grizzle 1990; Walters et al. 2001). Laboratory work was conducted at the Feller's House Field Station (28º54'N, 80º49'W), within the boundaries of Canaveral National Seashore.

Lift nets (species inventory)

I collaborated with Ms. Michelle Boudreaux, a graduate student at the University of Central Florida, to determine the number of sessile and mobile species on intertidal oyster reefs in Mosquito Lagoon. Ms. Boudreaux collected data on the sessile species. I focused on the mobile species, and that data are presented here.

A year-long species inventory was conducted with the use of lift nets (Figure 3). Methodology was adapted from Crabtree and Dean (1982), Coen et al. (1996), and Tolley et al. (2005). Lift net frames (1 m^2) were constructed from PVC pipe with a diameter of 3.8 cm. Delta Netting from the Memphis Net and Twine Company was used to create 0.5 m deep nets. The four sides of each net were made with 6.4 mm diameter mesh and the bottom was made with 1.6 mm diameter mesh. The smaller size netting was used to ensure that small organisms did not escape when the nets were retrieved. The netting was treated with green dip to provide salt resiliency. The sides and bottoms of each net were sewn together using a sewing machine and polyester core thread. Lastly, the netting was connected to the PVC frame with cable ties (50 lb test). Each net was held firmly in place by attaching four irrigation weights, one on each side, to the PVC frame with additional cable ties.

Six oyster reefs were selected within Mosquito Lagoon (Figure 4). Three reefs were in reference condition and three contained dead margins. On each reef, five replicate nets were deployed intertidally, just above mean low water. To protect against wave motion, the nets were placed on the protected, landward side of each reef. Upon deployment, 1.5 L of volume normalized oyster shells were placed within each net. Approximately 0.75 L were live oyster clusters and 0.75 L were single, disarticulated shells. All epifauna and epiflora were cleaned from the single, disarticulated shells but not the live clusters.

Lift nets were deployed for 13 months (June 2004 – July 2005), but data were only collected for 12 months (Table 1). The month of September 2004 was excluded due to hurricane activity.

The nets were retrieved at monthly intervals and surveyed for all fauna. Upon retrieval, all oysters within each net were brought back to the lab where all mobile species were identified, measured, and weighed. Live organisms were then returned unharmed to the Lagoon within 24 hours. Community metrics were determined, including density, biomass, diversity, and species richness. One specimen of each mobile species was preserved in 70% isopropanol to create a complete archive for Canaveral National Seashore. Observations of mobile species seen on oyster reefs but not collected in lift nets were also recorded to ensure that the inventory was as complete as possible.

Abiotic variables

On each collection date, temperature, salinity, and sediment accumulation were recorded. At each oyster reef, one temperature monitor (Onset Stowaway Tidbit Temperature Logger) was attached to a cinderblock with a cable tie. The loggers were submerged at the same water depth as the lift nets. Temperature was recorded hourly, and the mean temperature by month is presented. Salinity was measured using an optical refractometer (VeeGee A366ATC). The water sample was taken while standing beside the deployed lift nets on the dates when the nets were retrieved. Cylindrical sediment traps were constructed from PVC with a diameter of 10 cm, depth of 25 cm, and a cap securely sealed on the bottom (Lenihan 1999). Three sediment traps, submerged flush with the sediment, were evenly spaced between the lift nets at each site. During each month, sediment from the water column accumulated in the traps. During retrieval, a second cap was placed on the top of the sediment trap to prevent the loss of any water or sediment. New sediment traps replaced those collected. After collection, total sediment loads were determined by drying the samples in a drying oven (Econotherm Model Number 51221126) at 60º C for 48 hours. Samples were ground with a mortar and pestle and then separated into silt/clay and sand/grain fractions with a 0.062 mm sieve. Both fractions were then weighed on a top loading balance (O'Haus Scout 2-Model Number SC6010).

Statistical analyses

Community metrics were examined using a three factor nested analyses of variance (ANOVA) (SPSS 11.0). Normality (histogram) and homogeneity of variance (Levene's statistic) were tested prior to running all ANOVAs. For each ANOVA, the factors were reef type (fixed), site nested within reef type (random), and month (fixed). Lift nets were the residual. The response variables were: species richness (total number of species), diversity (Shannon-Wiener), density (number of individuals/lift net), and biomass (g). Tukey *post hoc* tests were run for ANOVAs when significant differences were found. For each species, the mean length (cm) and weight (g) were calculated.

To compare total sediment loads on reference reefs and reefs affected by dead margins, a three factor nested ANOVA was used. A three factor nested ANOVA was also used to compare the fraction of silt/clay on reference versus affected reefs. Again, normality (histogram) and variance (Levene's statistic) were tested. For both analyses, the factors were reef type (fixed), site nested within reef type (random), and month (fixed). Sediment traps were the residual. Tukey *post hoc* tests were run when significant results were found.

Results

Species inventory and community metrics

During this study, a total of 65 mobile species was found on oyster reefs within Mosquito Lagoon (Tables 2-3). Fifty-one species were collected using lift nets (Table 2) and an additional 14 species were observed by researchers apart from lift net collection (Table 3). The following phyla were represented: Chordata (24 species), Mollusca (20 species), Arthropoda (18 species), Echinodermata (2 species), and Annelida (1 species) (Tables 2, 3). Two species numerically dominated during all 12 collection months, the big-claw snapping shrimp *Alpheus heterochaelis* (2,489 individuals collected) and the flat-back mud crab *Eurypanopeus depressus* (1,217 individuals collected). It was observed that the number crab individuals were higher during the summer months, while the number of fish individuals peaked during the winter months. The ranges of species length and weight were larger for species that were collected in several different life phases, such as *Callinectes sapidus*, *Alpheus heterochaelis*, *Archosargus probatocephalus*, *Haemulon flavolineatum*, *Lagodon rhomboides*, and *Lutjanus griseus* (Table

2). Smaller measurements accounted for juveniles and larger measurements indicated adult sizes (Table 2).

Analyses of community metrics showed clear trends in Mosquito Lagoon. Reef type (reference or dead margins) did not have a significant influence on any of the following community metrics: species richness ($p = 0.985$), diversity ($p = 0.707$), density ($p = 0.624$), and biomass ($p = 0.940$) (Figures 5-8; Tables 4-7). However, site was significant for diversity ($p = 0.030$) and density ($p = 0.002$) (Tables 4-7). Month had a significant affect on all of the community metrics (all $p < 0.001$) (Tables 4-7). Species richness was highest in November, December, January, and May (Figure 5). Diversity was also highest during the months of November, December, January, and May (Figure 6). Density peaked during June, November, and December (Figure 7), while biomass was highest in June, November, December, and January (Figure 8).

Abiotic variables

During the 13-month study, temperatures in Mosquito Lagoon ranged from 16º C to 31º C (Figure 9). Salinity ranged from 25 to 35 ppt (Figure 10), falling within the typical average range of 25 to 45 ppt (Walters et al. 2001). Total sediment loads differed significantly between sites ($p = 0.011$), but not reef type ($p = 0.234$) (Figure 11; Table 8). After sediment loads were separated into fractions, percent silt/clay still did not differ significantly between reef type ($p = 0.454$) or sites ($p = 0.482$) (Figure 12; Table 9). During the months of June 2004 – June 2005, both sediment load and percent silt/clay differed temporally ($p = 0.004$ and < 0.001 respectively).

Tukey results showed sediment loads to peak in June 2004 while percent silt/clay fractions were highest in June 2004, July, and January (Figure 11-12).

Methods: Mini lift nets

Mini lift nets (species distributions within reefs)

Lift net methodology was modified to enable the placement of more nets to cover oyster reefs from the seaward edge to the landward edge of each reef. Smaller lift nets (0.25 m^2) (Figure 13) were constructed out of PVC with a diameter of 1.6 cm. A square (0.75 m^2) of Delta Netting with 1.6 mm diameter mesh was used to create a net with a depth of 0.25 m. It was attached to the PVC frame with cable ties.

Six oyster reefs were selected, three were reference reefs and three contained dead margins. Nine lift net were deployed at each site. They were arranged to cover three separate areas of each reef: the fore-reef (3 nets), mid-reef (3 nets), and back-reef (3 nets). Half a liter of oyster shells (0.25 L live and 0.25 L dead) were placed within each net. Nets were checked once a week for five successive weeks (Table 10). All mobile species collected in the nets were recorded. Their lengths (cm) and weights (g) were measured as well.

Statistical analyses

A three factor nested analysis of variance (ANOVA) was used to measure three community metrics: species richness (total number of species), density (number of individuals/lift net), and biomass (g). Normality (histogram) and homogeneity of variance

(Levene's statistic) were tested prior to running all ANOVAs. The main fixed factor was reef type (reference or dead margin), site was nested within reef type (random), area was nested within site (fixed), and mini lift nets were the residual. Tukey's *post hoc* tests were run when significant differences were found.

Results

All community metrics followed a similar pattern. Only two factors significantly affected species richness: reef type ($p = 0.009$) and area of the reef ($p < 0.001$) (Table 11). Density was significantly influenced by reef type ($p = 0.011$) and area of the reef ($p < 0.001$) (Table 12). Lastly, biomass was affected significantly by reef type ($p = 0.005$) and area of the reef ($p < 0.001$) (Table 13). Site was not significant for any of the community metrics (Tables 11-13).

Species richness, density, and biomass were significantly higher on reference reefs than affected reefs ($p < 0.001$) (Figures 14-16; Tables 11-13). Tukey *post hoc* tests revealed a pattern across the reef areas. For reference reefs, community metrics were highest on the fore-reef area, followed by the back-reef area, and with a significant drop in the mid-reef area (Figures 14-16). Conversely, reefs with dead margins had the highest community metrics on the back-reef area, followed by the fore-reef area, and with an even more drastic drop in the mid-reef area (Figures 14-16).

Twenty-four species were collected on the reference reefs, while 20 species were collected on reefs with dead margins (Table 14). Seventeen species (1 gastropod, 6 crustaceans, and 10 fishes) were found on the fore-reef area of reference reefs versus 15 species (3 gastropods, 7 crustaceans, and 5 fishes) collected on the fore-reef area of reefs with dead margins (Table 14). On the back-reef areas of reference reefs, 16 species were collected (5 gastropods, 5 crustaceans, and 6 fishes) while 18 species (4 gastropods, 8 crustaceans, and 6 fishes) were collected on the back-reef areas of reefs with dead margins (Table 14). The greatest difference in species distribution between reef type was seen on the mid-reef areas. For reference reefs, 8 species were recorded (1 gastropod, 5 crustaceans, and 2 fishes) versus zero species recorded for reefs affected by dead margins (Table 14).

Discussion

Similar community metrics were found on both reference reefs and reefs affected by dead margins. Due to the placement of the lift nets, these results focused solely on the back-reef areas of oyster reefs. Thus, the development of dead margins on oyster reefs in Mosquito Lagoon did not have a significant affect on the usage of back-reef areas by mobile and sessile species. This suggests that back-reef areas on affected reefs function similarly to reference reefs.

The assemblage of mobile and sessile species collected on oyster reefs within Mosquito Lagoon was similar to previous studies. Many of the mobile species collected on oyster reefs within Mosquito Lagoon were also found on oyster reefs in North Carolina (Meyer 1994; Breitburg 1999; Posey et al. 1999; Meyer and Townsend 2000), South Carolina (Coen et al. 1999), and along the southwest coast of Florida (Tolley et al. 2005). The two most abundant mobile species sampled within Mosquito Lagoon were the big-claw snapping shrimp *Alpheus heterochaelis* and the flat-back mud crab *Eurypanopeus depressus.* Likewise, previous studies found these two species to be abundant in temperate waters on both the Atlantic coast of North

Carolina (Meyer 1994) and the Gulf coast of Florida (Glancy et al. 2003). Just as Tolley et al. (2005) reported the replacement of temperate species by tropical cogeners, we observed the replacement of the striped blenny *Chasmodes bosquianus* (Breitburg 1999; Coen et al. 1999) by the Florida blenny *Chasmodes saburrae*.

The fifth most abundant mobile species collected was the green porcelain crab *Petrolisthes armatus*, considered an invasive exotic along the South Atlantic Bight (Knott et al. 2006; Glancy et al. 2003). Populations of this species can historically be found both in the Pacific (i.e. California to Peru) and the Atlantic (i.e. Africa, Ascension Island, Bermuda, Bahamas, Gulf of Mexico, West Indies, Caribbean, and South America down to Brazil) (Knott et al 2006). Although the exact pathway of introduction remains unexplained, possibilities include ballast transport and increasing winter temperatures, which favor its establishment (Knott et al. 2006). It was first collected along Florida's east coast in the 1930s at Biscayne Bay and Miami Beach (Knott et al. 2006). Slowly it spread northward, becoming well established in the Indian River Lagoon system (Knott et al. 2006). Studies have shown abundances to increase dramatically in only a few years after introduction (Knott et al. 2006). The current range of *P. armatus* along the South Atlantic Bight stretches from South Carolina down to the southern tip of Florida (Knott et al. 2006).

Several juvenile nekton (i.e. transient) species were collected in the lift nets within Mosquito Lagoon, including the pinfish *Lagodon rhomboides* (length range: 2.3 – 7.7 mm), sheepshead *Archosargus probatocephalus* (length range: 4.4 – 9.7 mm), and gray snapper *Lutjanus griseus* (length range: 3.0 – 11.2 mm) (Table 2). These commercially and recreationally valuable species were also found on the west coast of Florida (Tolley et al. 2005).

Community metrics for the mobile species were similar to those found by Tolley et al. (2005) along the southwest coast of Florida. Species richness (Mosquito Lagoon: ~ 3-7 species; southwest FL: ~ 4-11 species) and diversity (Mosquito Lagoon: ~ 0.6-1.6; southwest FL: ~ 0.3-1.7) were found to be in the same range. Biomass (Mosquito Lagoon: ~ 13-30 g; southwest FL: ~ 17-85 g) and density (Mosquito Lagoon: ~ 12-40 individuals/lift net; southwest FL: ~ 20-400 individuals/m^2) were lower in Mosquito Lagoon. In both systems, there were more fish species than decapod crustaceans. Along the Gulf coast (i.e. the Caloosahatchee, Estero, and Faka-Union estuaries), 16 fish species and 9 decapod crustacean species were recorded. In Mosquito Lagoon, the numbers were slightly higher with 23 fish species and 18 decapod crustacean species (Table 2). Although there were more fish species in both systems, decapod crustaceans dominated numerically and in terms of biomass.

Previous research in Mosquito Lagoon documented an increase in sediment accumulation on the seaward edges (i.e. fore-reef area) of reefs affected by dead margins (Wall et al. 2005). Subsequently, increases in sediment loads were linked with decreases in the survival of newly recruited *Crassostrea virginica* (Wall et al. 2005). Thus, it was expected that differences in sediment loads would affect the species assemblages found on reference reefs and those affected by dead margins. However, my study focused on the landward edges (i.e. back-reef areas) of oyster reefs, and I found no significant differences in sediment loads or silt/clay fractions. This suggests that dead margins protect back-reef areas from boat wakes and that back-reef areas are similar to reference reefs.

Although dead margins did not affect species biodiversity on back-reef areas of oyster reefs, they did affect the distribution of species. Species richness, density, and biomass were significantly higher on reference reefs than reefs with dead margins (Figures 14-16; Tables 11-13). This can be attributed to the drastic drop in all three community metrics on the mid-reef areas of affected reefs. The mid-reef areas of affected reefs were situated above mean high water and were exposed at all times. It is hypothesized that the absence of all mobile species was due to a lack of water, shade, and topographic complexity. Similar community metrics were found on the fore-reef and back-reef areas within reef type and between reef types (Figures 14-16; Tables 11-13). These areas are continuously submerged throughout the tide cycle. Dead margins may provide a barrier against wave motion and sedimentation, creating a favorable environment for mobile species to inhabit.

In conclusion, dead margins significantly affected the mobile species community on oyster reefs within Mosquito Lagoon. Although biodiversity was found to be similar on both reef types, this can only be interpreted as similar functioning between reference reefs and the back-reef areas of reefs with dead margins. The remaining reef surface (i.e. fore-reef and mid-reef areas) showed drastic differences in species distributions. Thus, the area species chose to inhabit decreased on reefs with dead margins. Over time, this may hinder the ability of oyster reefs to act as biogenic habitats and subsequently reduce biodiversity in Mosquito Lagoon.

CHAPTER TWO: REEF ARCHITECTURE AND SUBSEQUENT AFFECTS ON PREDATION SUCCESS

Introduction

Oyster reefs in Mosquito Lagoon

Mosquito Lagoon, the northernmost portion of the Indian River Lagoon, lies within Canaveral National Seashore (CANA) on the east coast of central Florida (Provancha et al. 1992; Walters et al. 2001). Located along the border between tropical and temperate climates, Mosquito Lagoon is rich in diversity (Walters et al. 2001). It acts as a refuge for 14 federally listed threatened and endangered species, is nationally recognized for recreational fishing, and is the southernmost limit along the Atlantic coast for undisturbed, intertidal reefs of the eastern oyster *Crassostrea virginica* (Grizzle and Castagna 1995; Walters et al. 2001).

Much of Mosquito Lagoon's diversity and productivity can be attributed to its intertidal oyster reefs (Walters et al. 2001). Oysters are considered keystone species and ecosystem engineers, acting as havens of biodiversity for fish, crab, shrimp, and gastropod species (Wells 1961; Paine 1969; Purchon 1977; Jones et al. 1994; Dame 1996; Coen and Luckenbach 2000). Generations of oysters build upon one another to create increasingly complex three-dimensional reefs (Dame 1996). These structures offer a variety of microhabitats for estuarine species to inhabit (Sellers and Stanley 1984; Dame 1996; Bartol et al. 1999; Micheli and Peterson 1999; Coen and Luckenbach 2000). Oyster reefs also actively contribute to ecological processes within Mosquito Lagoon (Smithsonian Institution 2001). While reefs stabilize the sediment and influence water currents, individuals help improve water quality by filtering out contaminants and pollution (Loosanhoff and Nomejko 1946; Bahr and Lanier 1981; Lenihan 1999; Gosling 2003; Nelson et al. 2004).

Recently, concern has arisen for the survival and viability of *C. virginica* reefs located in Mosquito Lagoon. Since 1943, recreational boating activity has caused atypical mounds of disarticulated shells (dead margins) to emerge on the seaward edges of oyster reefs located along major navigational channels (Grizzle and Castagna 1995; Grizzle et al. 2002). These dead margins have led to differences in reef architecture, which may in turn affect the functional integrity of oyster reefs (Grizzle et al. 2002). Reefs in reference condition are flat and completely submerged at high tide. Oysters are oriented perpendicular to the substrate. However, reefs that are affected by dead margins contain dead, disarticulated oyster shells that lay horizontally on the substrate. These shells form mounds that are exposed throughout the tide cycle, creating a steep slope on the seaward edge. Once dead margins are formed, little is known about their influence on the biotic interactions of oyster reef communities.

Predation

The biological process of predation is regarded as one of the foremost factors in benthic community structuring within estuaries (e.g. Mackin 1959; Hines et al. 1990; Wilson 1990; Eggleston et al. 1992; Micheli 1997). A principal source of natural mortality in bivalve mollusks, predators influence the size structures of oyster populations and affect overall abundance and distribution patterns (Gosling 2003). Predator species focus on different phases of an oyster's life-cycle (Kennedy 1991). It is estimated that 99% of oyster larvae are lost before settlement (Kennedy 1991). This is primarily due to predation, particularly by planktivores (e.g.

ctenophores, anemones, and some larval fish) (Kennedy 1991). Oyster larvae that successfully settle are called spat. Carnivorous worms and small crabs, such as mud crabs and juvenile blue crabs, become the main predators at this point (Bisker and Castagna 1987; Eggleston 1990; Dame 1996). Lastly, adult blue crabs, whelks, oyster drills, rays, and several sciaenid fish (e.g. red and black drum) prey on larger spat and small adult oysters (Dame 1996).

My study documented the ecological implications of dead margins on *C. virginica* reefs by focusing on reef architecture and its affect on predation success. Comparisons were made between vertical profiles and live oyster densities of reefs in reference condition and reefs that contained dead margins. Affects on predation success were measured in a manipulative field experiment altering the following parameters: overall vertical slope, shell configuration, and shell orientation.

Methods: Reef profiles

Reef profiles

To document structural differences, two types of transects were run along five reference reefs and five reefs with dead margins within Mosquito Lagoon, Florida. All transects were run during the summer and fall of 2005. First, quadrat transects (Figure 17) determined the percent of live oysters, the percent of shell clusters, surface topography, and the angle of shells on each reef type. On each reef, three transect lines (length: 10 m) were stretched parallel to the water line and covered the three areas of the reef: the fore-reef, mid-reef, and back-reef. Quadrats (0.25 m^2) were placed at five randomly selected points along each transect line. The quadrats were alternatively placed either above or below the transect line. A chain was carefully laid across the middle of the quadrat to measure topography. Chain links within the quadrat were counted and recorded. The angles of all shells within each quadrat were measured using a Johnson's Magnetic Angle Locator. Lastly, all oysters in the quadrats were classified as either live or dead and single or clustered.

Laser transects (Figure 18) were used to record reef profiles. A transect line was stretched from the seaward edge to the landward edge of each reef. A laser level (Johnson 9100/40-0909) was secured to a tripod and placed at the seaward edge of the transect line. Every 20 cm, the distance between the lagoon bottom and the top of the reef was recorded by locating the laser beam on a stadia rod. This was repeated ten times along the length of each of the ten reefs. See Wall et al. (2005) for additional details.

Statistical analyses

Three factor nested analyses of variance (ANOVA) were used to compare the percent of live oysters, the percent of shell clusters, topographic complexity, and shell angles on three reef areas (fore-reef, mid-reef, and back-reef) on reference reefs versus reefs with dead margins. Normality (histogram) and homogeneity of variance (Levene's statistic) were tested prior to running all ANOVAs. The main fixed factor was reef type (reference or dead margin), site was nested within reef type (random), area of reef was nested within site (fixed), and quadrats were the residual. In order to compare the slopes of reference reefs versus those with dead margins, a one factor ANOVA was run. Tukey's *post hoc* tests were conducted when significant results were found.

Results

The percent of live oysters was significantly affected both by reef type ($p < 0.001$) and area of reef ($p < 0.001$) but not site ($p = 0.621$) (Table 15). Reference reefs had significantly more live oysters than reefs with dead margins (Figure 19). According to the Tukey *post hoc* test, reference reefs contained similar amounts of live oysters on the fore-reef and back-reef areas with a slight drop in the mid-reef area ($p = 0.005$) (Figure 20). Affected reefs contained the most live oysters on the back-reef and fore-reef areas while mid-reef areas contained more dead oyster shells ($p < 0.001$) (Figure 20).

The percent of shell clusters was significantly affected by reef type ($p < 0.001$) and area of reef ($p < 0.001$), but not site ($p = 0.428$) (Table 16). Again, reference reefs contained significantly more oyster clusters than reefs affected by dead margins (Figure 21). The Tukey *post hoc* tests revealed that for reference reefs, all three reef areas contained similar amounts of shell clusters ($p = 0.408$). Reefs with dead margins, however, contained more shell clusters on the back-reef area compared to the fore-reef and mid-reef areas ($p < 0.001$) (Figure 22).

The number of chain links per quadrat was significantly affected by reef type ($p = 0.038$) and area of reef ($p < 0.001$), but not site ($p = 0.134$) (Table 17). Reference reefs had a significantly higher mean number of chain links than affected reefs (Figure 23). Thus, reference reefs had greater structural complexity. Area of reef did not have a significant affect on the number of chain links for reference reefs ($p = 0.908$), however, it did on reefs with dead margins ($p = 0.022$) (Table 17; Figure 24). The fore-reef and back-reef areas were similar, while a decrease in topographic complexity was documented on the mid-reef area.

The orientation (i.e. angle) of shells ranged from 0 to 90 degrees. Shells at 0º were horizontal to the surface of the oyster reef while shells at 90º were perpendicular to the surface of the oyster reef. Sixty-eight percent of shells on affected reefs were < 20º, while 66% of shells on reference reefs were ≥ 20º (Figure 25). Thus, 20º was set as the border between low and high angle measurements. The percent of high angles (i.e. ≥ 20º) was significantly affected by reef type ($p = 0.006$) and area of reef ($p < 0.001$), but not site ($p = 0.080$) (Table 18). Reference reefs had significantly more high angles than affected reefs (Figure 26). The three reef areas were similar on reference reefs ($p = 0.216$), however, the fore-reef and back-reef areas of affected reefs contained more high angles than the mid-reef area ($p = 0.001$) (Figure 27).

Profiles of the overall reef slopes differed between reference reefs and those with dead margins. The widths of affected reefs were significantly more compressed (mean width: 760 ± 51) than reference reefs (mean width: 1168 ± 141) ($p = 0.026$) (Figures 28-29; Table 19). The peaks of affected reefs were significantly higher (mean height: 43.8 ± 6.4) than reference reefs (mean height: 21.4 ± 4.4) ($p = 0.021$) (Figures 28-29; Table 20). The mean of the overall slope for each reef type depicted the differences clearly (Figure 30). The fore-reef areas of affected reefs had steep slopes ranging from 1.6 to 2.6 (Figure 31) while those of reference reefs only ranged from 0.5 to 1.4 (Figure 32). The mean slope of the fore-reef area was calculated by taking the mean of all the fore-reef profiles for each reef type and then calculating the slope of the subsequent line. The results showed that the fore-reef area of affected reefs ($m = 2.0$) was approximately double that of reference reefs ($m = 1.0$) (Figure 33). Slope was significantly different between the two reef types ($p = 0.002$) (Table 21).

Methods: Predator enclosures

Predator enclosures

Two oyster reefs were selected within Mosquito Lagoon. Both reefs contained well-developed dead margins of equal slope (m = 2.0). Five-sided enclosures were constructed out of 1.0 mm Vexar mesh. Five squares (0.5 m^2) of Vexar were woven along their edges with cable ties to create enclosures with open tops. Thirty-six enclosures, divided into two rows, were deployed on each oyster reef (Figure 34). The first row was lined up along the sloped portion of the fore-reef area, at the edge of mean low water. At low tide, one-fourth (0.05 m) of each enclosure was covered with water. The second row was placed on the flat portion of the fore-reef area. At low tide, half (0.25 m) of each enclosure was covered with water. Once deployed, the enclosures were secured with four irrigation weights, one connected to each corner.

Within the five-sided enclosures, three variables of reef architecture were manipulated (Figure 34): (1) overall reef slope (sloped or flat), (2) shell configuration (single or clustered), and (3) shell orientation (vertical or horizontal). These manipulations were conducted in order to tease apart the affects of architecture on predation rates on juvenile oysters. After creating all possible combinations, the following six treatments were deployed: (1) Flat-Single-Vertical, (2) Sloped-Single-Vertical, (3) Flat-Single-Horizontal, (4) Sloped-Single-Horizontal, (5) Flat-Clustered, and (6) Sloped-Clustered (Figure 34). Each treatment was replicated 3 times and matched with three controls (i.e. enclosures with the same shell manipulation as each treatment, but which did not contain a predator).

Disarticulated oyster shells were collected from Mosquito Lagoon. Twelve shells, scraped clean of all epifauna and epiflora, were placed within each enclosure. One juvenile oyster (diameter: 5-10 mm) was present on each shell. In order to create shell clusters, three single shells were linked together with a cable tie, resulting in four shell clusters per enclosure. Vertical orientation was achieved by attaching single oyster shells perpendicular to a flat piece of Vexar (1 m^2) with cable ties. Each oyster shell had a hole drilled into the corner. This Vexar mesh was then placed at the bottom of an enclosure. Horizontal shells were placed flat on the Vexar bottom of the enclosures.

Three predators were used in separate trials: the blue crab *Callinectes sapidus*, the common mud crab *Panopeus herbstii*, and the Atlantic oyster drill *Urosalpinx cinerea* (Figure 35). Before each trial, predators were starved for 24 hours. Predators were placed in 18 of the enclosures; the remaining 18 were used as controls. Controls were used to determine if oyster mortality resulted solely from predation or involved other factors. Trials lasted 6 days and were repeated three times for each predator species at each of the two sites. After each trial, the numbers of dead juvenile oysters were counted. Trials were run from June to September 2005.

Statistical analyses

Exploratory analysis was conducted using contingency tables to compare the effects of all variables and their interactions on oyster mortality. Significance was determined using Pearson's chi-square test. The results showed that only two variables significantly affected oyster mortality: predator species and trial date. Thus, the analyses in this paper focused solely on these two variables. In order to correctly analyze the remaining variables, further replication is necessary.

Contingency tables were created to compare the affects of species, trial, and the interaction between both variables on oyster mortality. Significance was tested using Pearson's chi-square analysis. Log linear models were also created and tested against reference models to fully examine the influence of each variable.

Results

According to the contingency tables and Pearson's chi-square test, predator species and trial number significantly affected oyster mortality (both $p < 0.001$). In descending order, the common mud crab *Panopeus herbstii* consumed the most juvenile oysters (52%), then the Atlantic oyster drill *Urosalpinx cinerea* (31%), and lastly the blue crab *Callinectes sapidus* (16%) (Figure 36; Table 22). Although these were the overall results, the dominant predator within trials varied. In the first trial, *P. herbstii* consumed the most oysters ($p < 0.001$), while in the third trial, *U. cinerea* consumed the most oysters ($p < 0.001$) (Figure 37; Tables 23). There was not a significant difference in the second trial between predator species ($p = 0.372$) (Figure 37; Tables 23). Three log linear models (i.e. mortality*species, mortality*trial, and mortality*species*trial) were shown to be significant (Table 24). No mortality was recorded within the controls.

Temperature and rainfall data for June – September 2005 was obtained from the National Climatic Data Center (NOAA 2005). Mean monthly temperatures were as follows: June (23.2ºC minimum; 29.3ºC maximum), July (24.3ºC minimum; 32.2ºC maximum), August

(24.3ºC minimum; 33ºC maximum), and September (23.4ºC minimum; 30.8ºC maximum). Precipitation levels peaked in June (347.2 mm), dropped in July (69.3 mm), and were similar during August (109 mm) and September (186.7 mm).

Discussion

Reference reefs had greater topographic complexity than reefs with dead margins. They had approximately four-fold more live oysters, twice as many shell clusters, and twice as many shells angled ≥ 20 degrees (Figures 19, 21, 26). This suggests that the development of dead margins greatly reduced the 3-dimensional structure and interstitial heterogeneity of reef architecture. Significant differences were observed across the profile of the reefs. The percent of live oysters was greatest on the fore-reef and back-reef areas (Figure 20). These areas are submerged longer and exposed for less time than mid-reef areas, which aids the growth and survival of live oysters by allowing them to filter-feed for longer periods of time (Loosanhoff 1932; Ingle and Dawson 1952; Burrell 1982; Roegner and Mann 1995; Bartol et al. 1999). Fore-reef and mid-reef areas potentially protect back-reef areas, creating a buffer against wave motion, sedimentation, and the accumulation of disarticulated oyster shells. The greatest difference in shell angle occurred between mid-reef and back-reef areas of both reef types, the latter having a greater percentage of shells angled ≥ 20 degrees (Figure 27). Again, this increase in vertical complexity may be due to the buffering actions of the fore-reef and mid-reef areas.

Not only did dead margins affect the structural complexity of oyster reefs, but they also altered vertical reef profiles. Overall, the development of dead margins compressed the widths and increased the center peaks of oyster reefs (Figure 30). A significant difference was documented between the slopes of the fore-reef area on reference reefs and those affected by dead margins (Table 21). Affected reefs had slopes that were twice as steep as reference reefs (Figure 33). These findings parallel previous research done in the area. Wall et al. (2005) showed a significant difference in reef elevation between reference reefs (mean: 28.63 ± 2.29 cm) and those with dead margins (mean: 53.63 ± 3.98 cm) ($p = 0.0016$).

The architectural structure of biogenic habitats, such as oyster reefs, greatly affects their ecological functioning (Bell and Hicks 1991; Bell et al. 1991). The designation of *Crassostrea virginica* as an ecosystem engineer reveals the importance of reef structure to the surrounding community's biodiversity (Paine 1969; Dame 1996; Lenihan and Peterson 1998; Coen and Luckenbach 2000). Increasing species richness can often be attributed to high habitat complexity (MacArthur and MacArthur 1961; Murdoch et al. 1972; Leather 1986). Reef structures provide refugia along interstitial and tidal gradients for both juvenile oysters and other estuarine species (Bartol et al. 1999). This refugia protects species from environmental stressors such as predation (Nichy and Menzel 1967; Menge and Lubchenco 1981; Summerson and Peterson 1984), dessication (Wells 1961; Bahr and Lanier 1981), sediment deposition (Grant et al. 1990), and hypoxia (Seliger et al. 1985; Breitburg 1992; Lenihan and Peterson 1998). Thus, any changes in reef architecture would be expected to influence biotic communities and subsequently the biological interactions among species.

Previous studies have shown changes in habitat to affect predator-prey interactions (Lipcius and Hines 1986; Seitz et al. 2001; Woodley and Peterson 2003; Grabowski 2004; Griffen and Byers 2006). Habitat complexity reduces predator foraging efficiency, increases refuge for prey species, and provides protection for intermediate predators within intraguild predation systems (Gause 1934; Huffaker 1958; Jackson et al. 2001; Byers 2002; Griffen and Byers 2006). In North Carolina, enhanced habitat complexity of oyster reefs weakened the trophic interactions between the oyster toadfish *Opsanus tau*, the mud crab *Panopeus herbstii*, and the eastern oyster *Crassostrea virginica* (Grabowski 2004). Vertically complex oyster reefs allowed *P. herbstii* to escape *O. tau* predation and also increased the survival of juvenile *C. virginica* (Grabowski 2004).

My study also focused on the interaction between juvenile oysters and three dominant predators. Contrary to expectations, complexity variables (i.e. overall reef slope, shell configuration, and shell orientation) did not have a significant influence on oyster mortality. However, a significant difference was established between mortality caused by species and by trial date (Tables 20-23). The common mud crab *Panopeus herbstii* was shown to be the more dominant predator in this system (Figure 36). Differences between monthly levels of precipitation may account for the variation seen during the trial dates.

In conclusion, a decrease in habitat complexity on oyster reefs affected by dead margins was documented. It is hypothesized that these reefs have reduced ecological functioning (i.e. impaired filtering capacity and diminished biogenic habitat area) and may contribute less to the estuarine community within Mosquito Lagoon than reference reefs. Although manipulative experiments did not show a change in predation of juvenile oysters according to structural variables, further research is necessary to rule out disruptions of biological interactions. Determining the full affects of dead margins is vital to the preservation and maintenance of oyster reef habitats within Mosquito Lagoon.

APPENDIX A – FIGURES

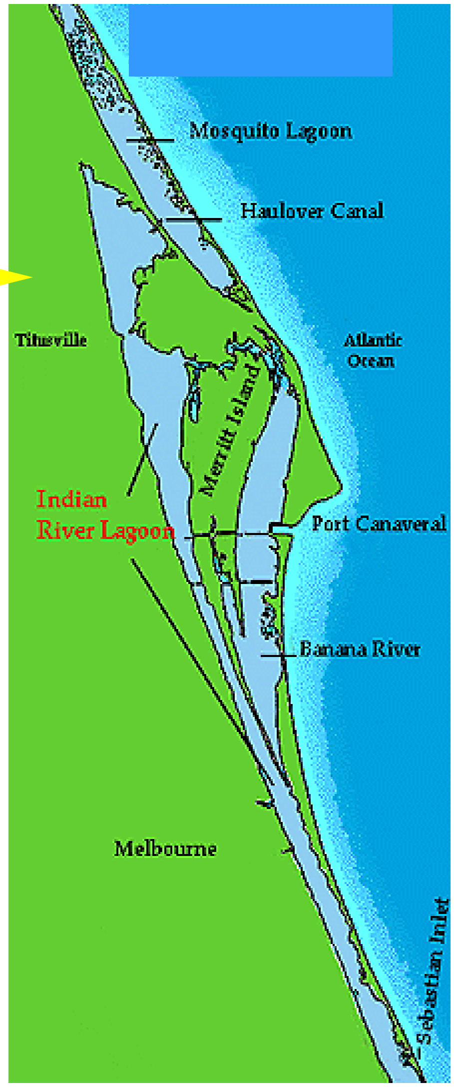

Figure 1. The Indian River Lagoon system.

The IRL consists of Mosquito Lagoon, the Banana River, and the Indian River (SeaWorld 2002; NOAA 2006).

Figure 2. Oyster reefs found within Mosquito Lagoon, Florida.

On the left is a reference reef with no dead margins. On the right is an affected reef that has developed a mound of dead, disarticulated shells on the seaward edge.

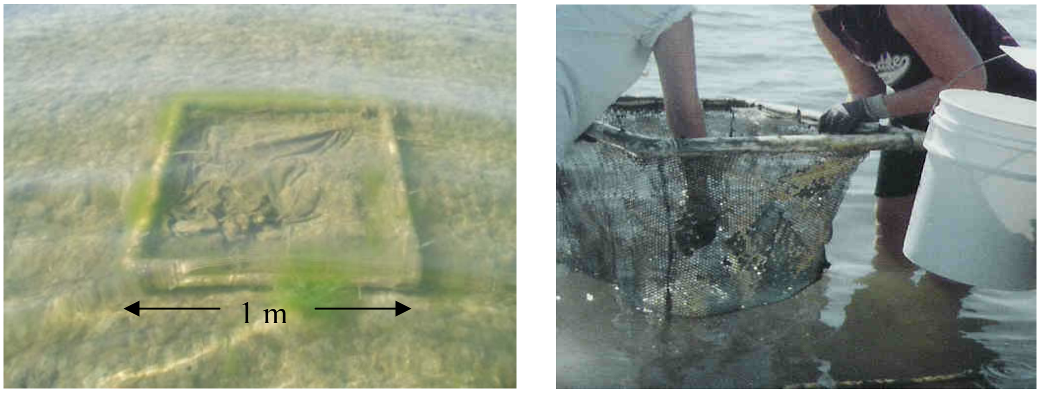

Figure 3. Lift nets ($1m^2$) upon deployment (left) and retrieval (right).

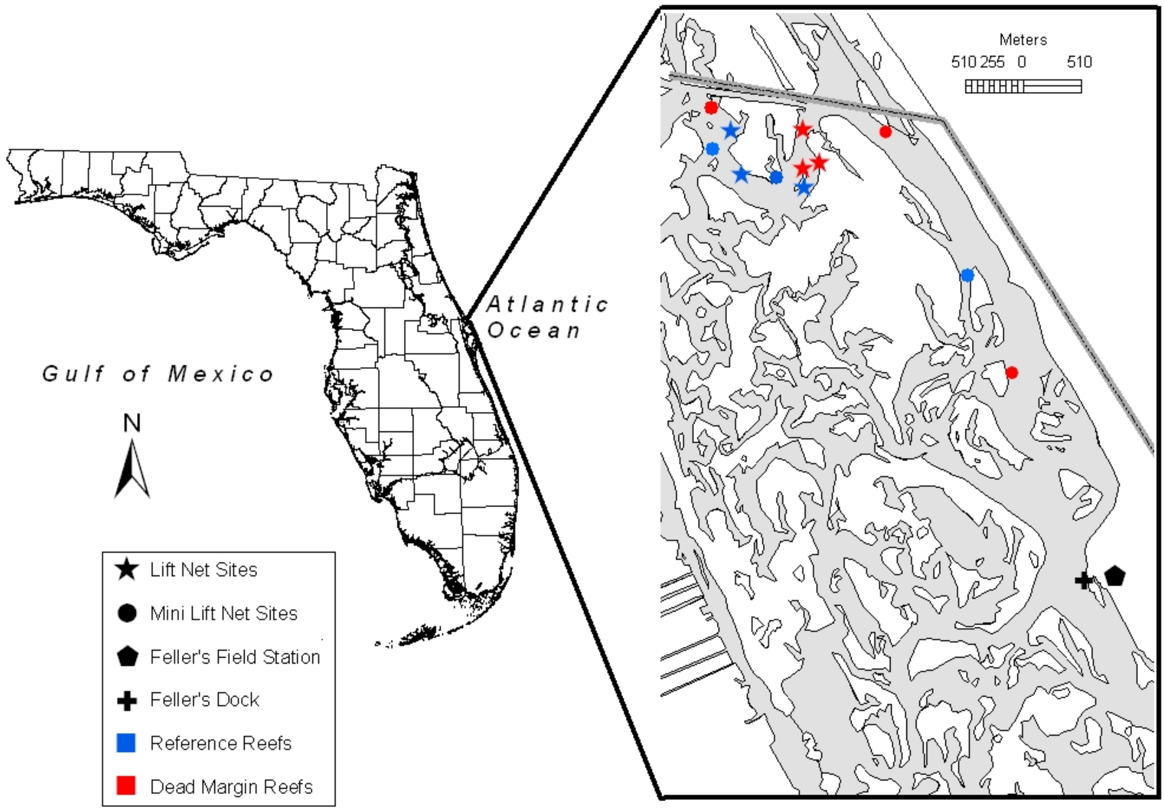

Figure 4. Oyster reefs selected for lift net and mini lift net deployment.

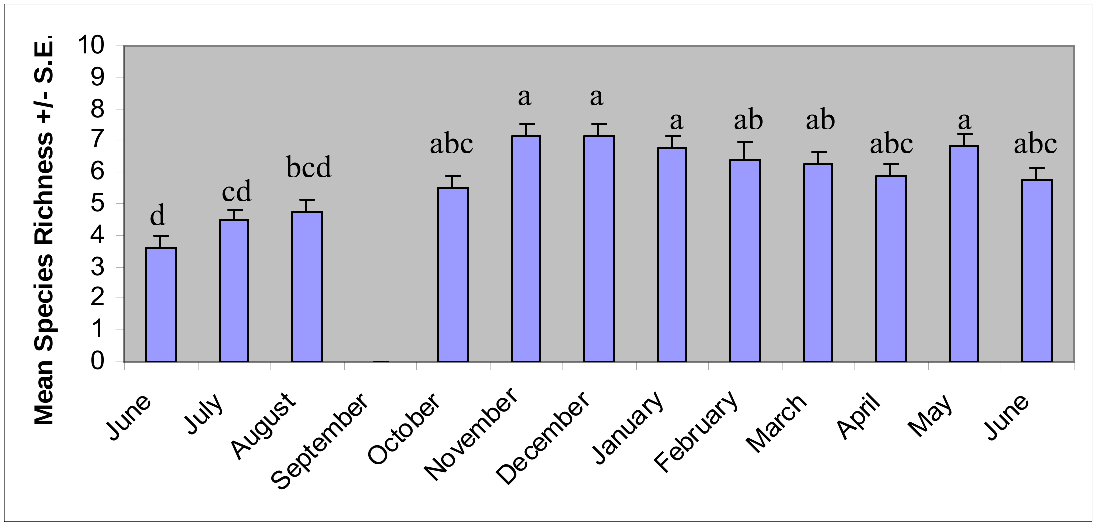

Figure 5. Mean species richness (total number of mobile species) (± S.E.) on oyster reefs within Mosquito Lagoon for June 2004 - June 2005.

Data are missing from the month of September due to hurricane activity. Lower case letters refer to the differences between months at the p ≤ 0.5 level according to Tukey *post hoc* comparisons.

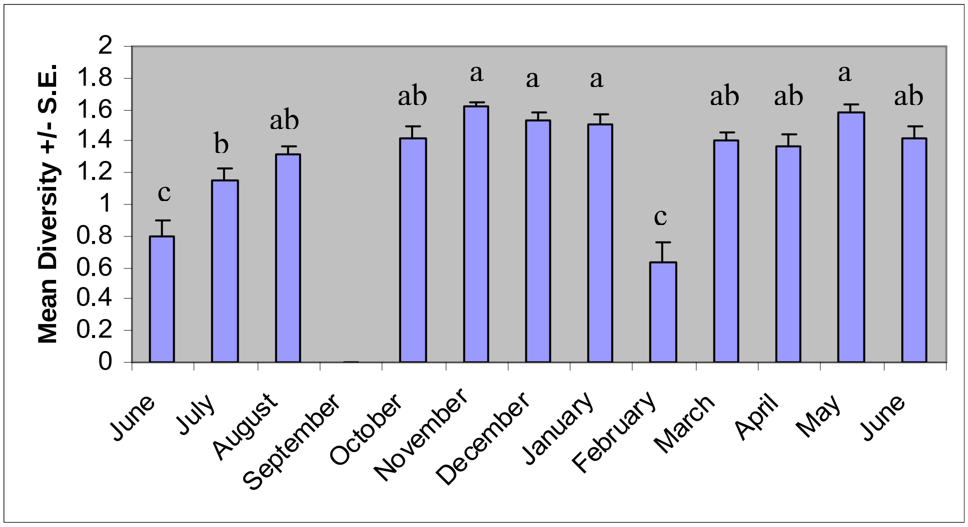

Figure 6. Mean diversity (Shannon-Weiner) (± S.E.) of mobile species found on oyster reefs within Mosquito Lagoon for June 2004 - June 2005.

Data are missing from the month of September due to hurricane activity. Lower case letters refer to the differences between months at the $p \leq 0.5$ level according to Tukey *post hoc* comparisons.

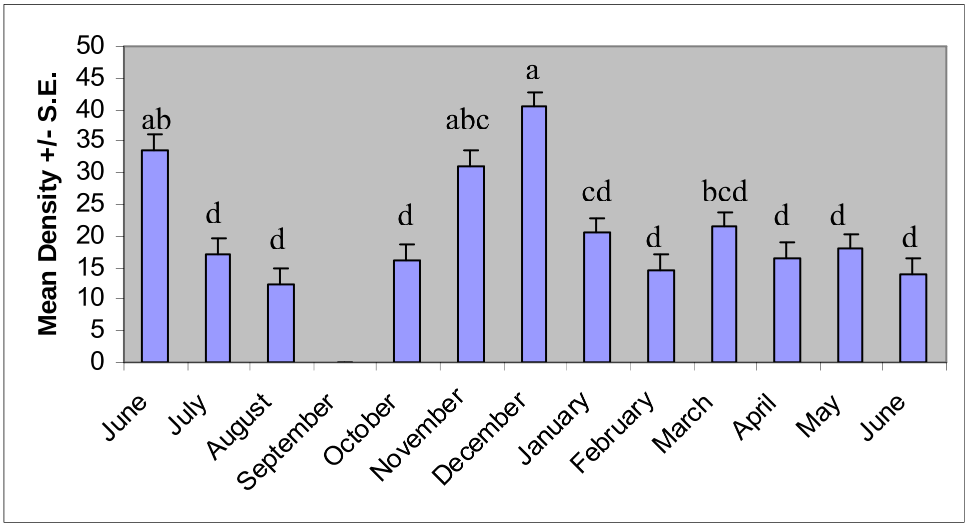

Figure 7. Mean density (total number of individuals/lift net) (± S.E.) of mobile species found on oyster reefs within Mosquito Lagoon for June 2004 - June 2005.

Data are missing from the month of September due to hurricane activity. Lower case letters refer to the differences between months at the $p \leq 0.5$ level according to Tukey *post hoc* comparisons.

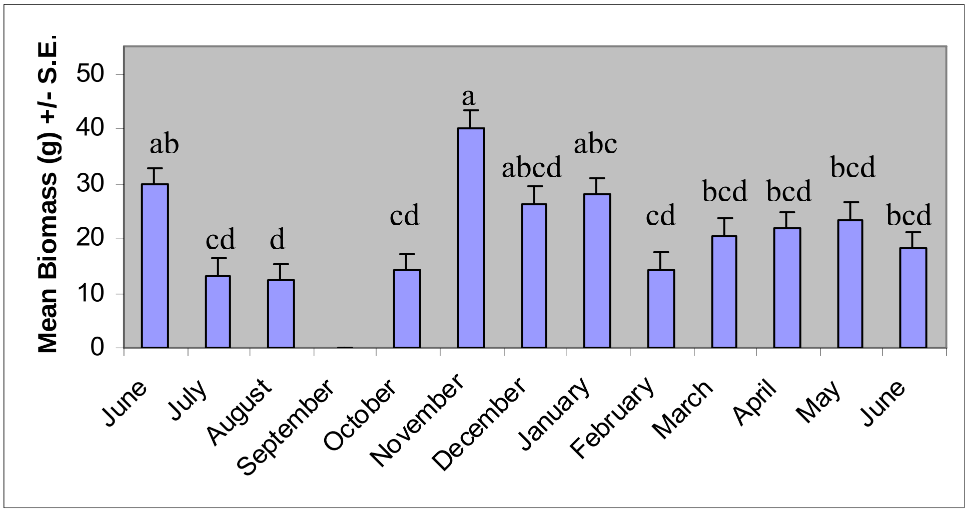

Figure 8. Mean total biomass (g) (± S.E.) of mobile species found on oyster reefs within Mosquito Lagoon for June 2004 - June 2005.

Data are missing from the month of September due to hurricane activity. Lower case letters refer to the differences between months at the $p \leq 0.5$ level according to Tukey *post hoc* comparisons.

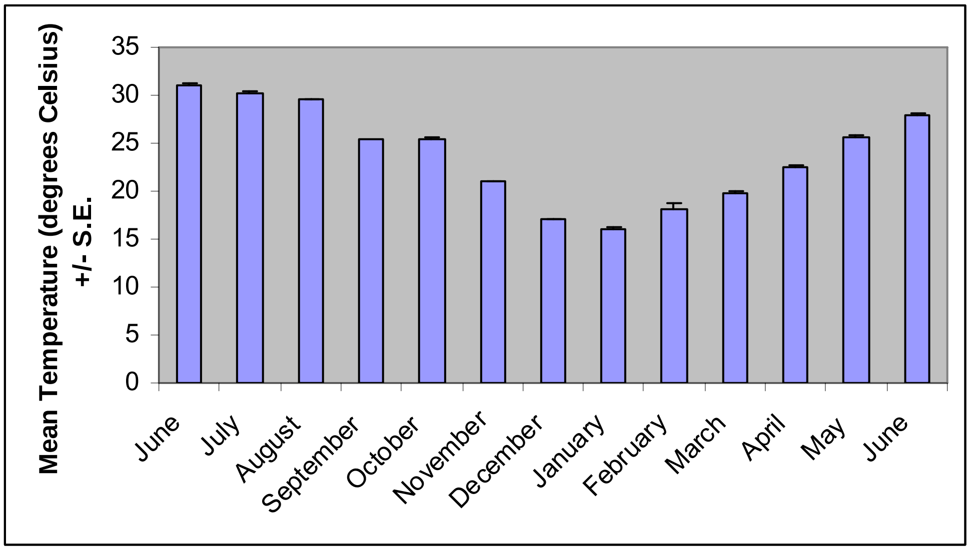

Figure 9. Mean temperature (± S.E.) measured at each site on lift net retrieval dates.

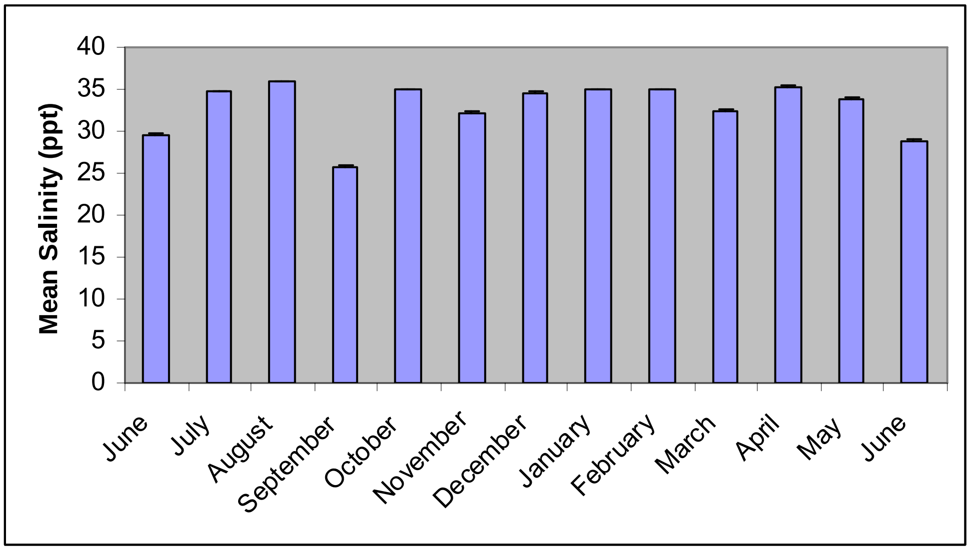

Figure 10. Mean salinity (± S.E.) measured at each site on lift net retrieval dates.

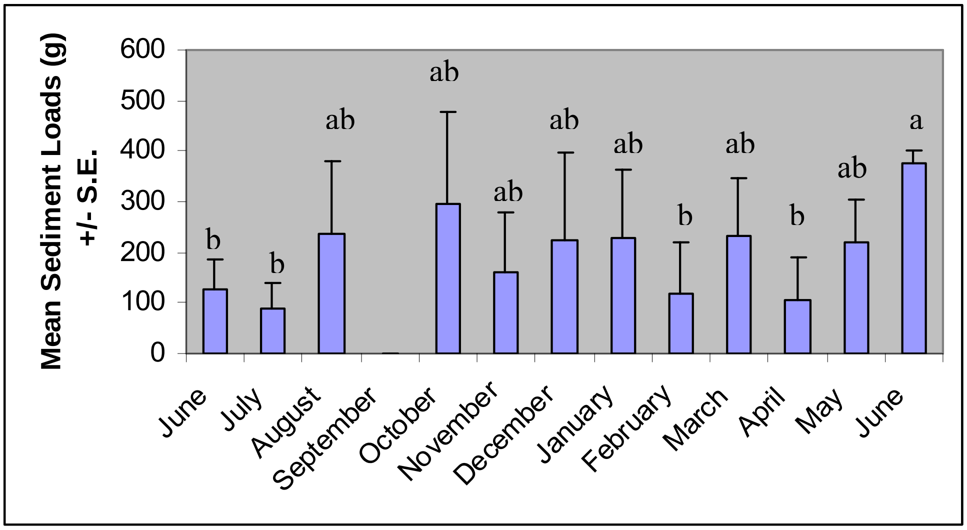

Figure 11. Mean sediment loads (± S.E.) collected at lift net sites per month.

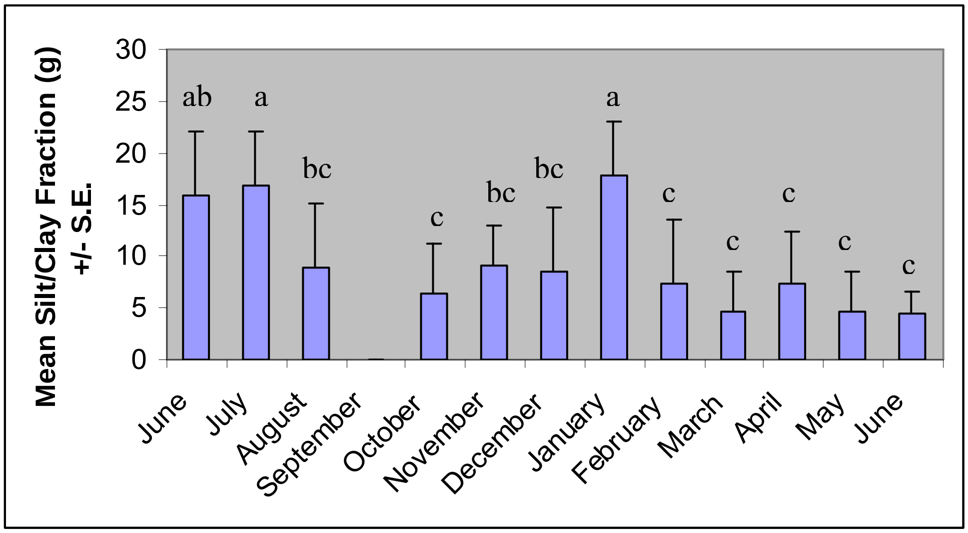

Figure 12. Mean silt/clay fraction (± S.E.) of the total sediment loads collected at lift net sites per month.

Lower case letters refer to the differences between months at the $p \leq 0.5$ level according to Tukey *post hoc* comparisons.

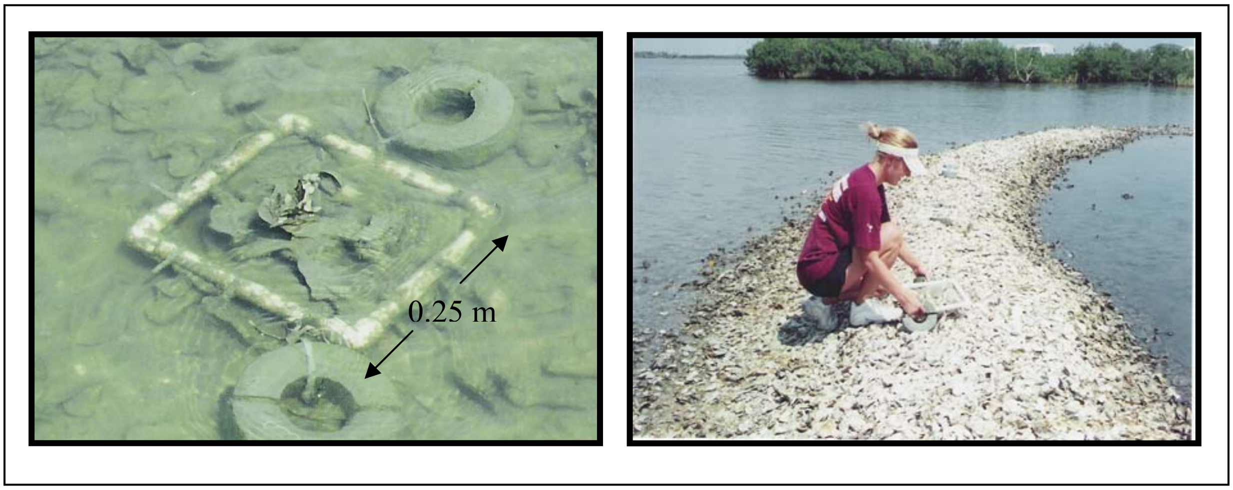

Figure 13. Deployment of mini lift nets (0.25 m^2) in Mosquito Lagoon.

.

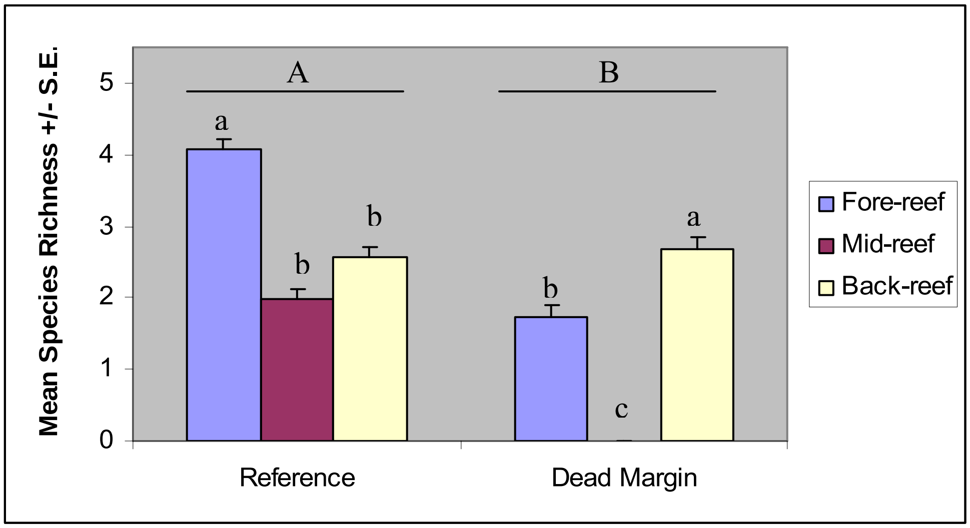

Figure 14. Mean species richness (total number of mobile species) (± S.E.) found on three areas of oyster reefs in reference condition and those with dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* comparisons. Lower-case letters refer to Tukey *post hoc* comparisons between the reef areas of reference reefs and reefs with dead margins (analyzed separately).

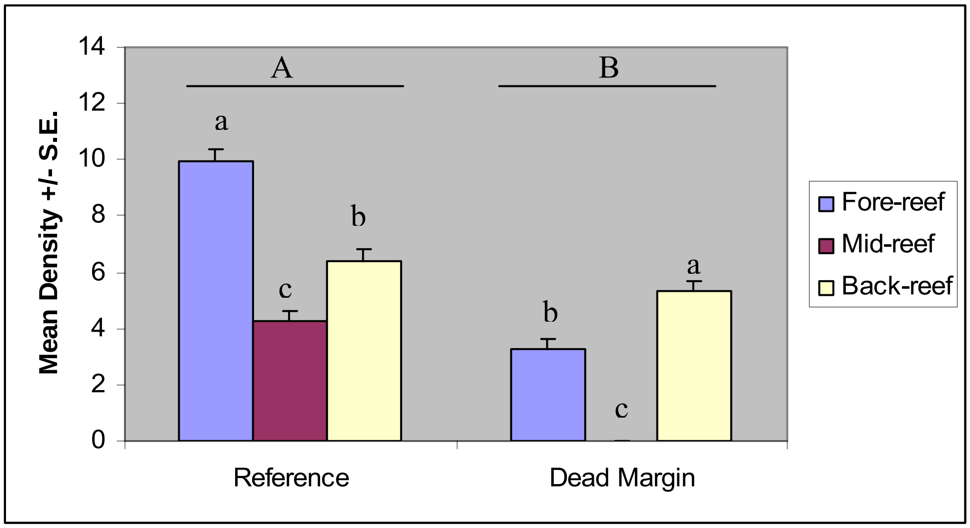

Figure 15. Mean density (number of individuals/mini lift net) (± S.E.) found on three areas of oyster reefs in reference condition and those with dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* comparisons. Lower-case letters refer to Tukey *post hoc* comparisons between the reef areas of reference reefs and reefs with dead margins (analyzed separately).

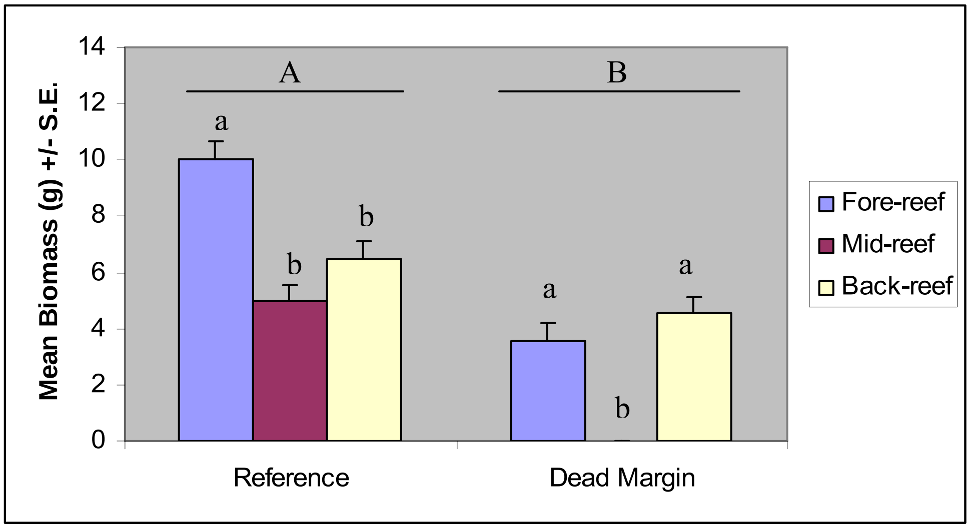

Figure 16. Mean biomass (g) (± S.E.) found on three areas of oyster reefs in reference condition and those with dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* comparisons. Lower-case letters refer to Tukey *post hoc* comparisons between the reef areas of reference reefs and reefs with dead margins (analyzed separately).

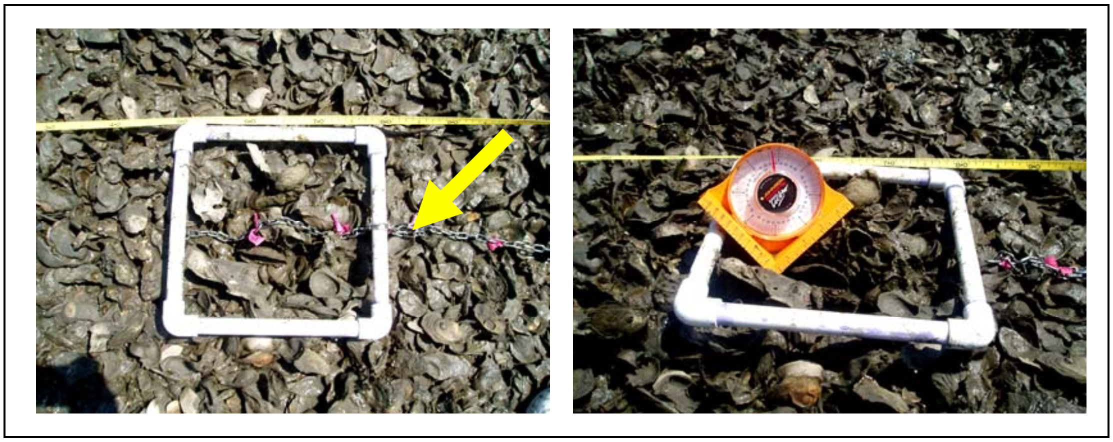

Figure 17. Tools used during quadrat transects: transect tape, 0.25 m^2 quadrat, chain marked every 10 cm (yellow arrow), and Johnson Magnet Angle Locator.

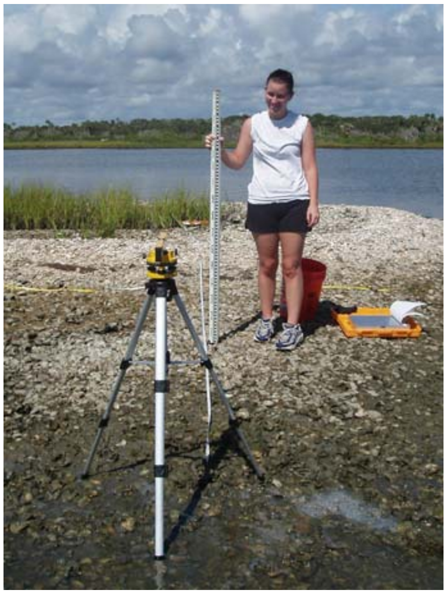

Figure 18. Tools used during laser transects: transect line, stadia rod, and laser level.

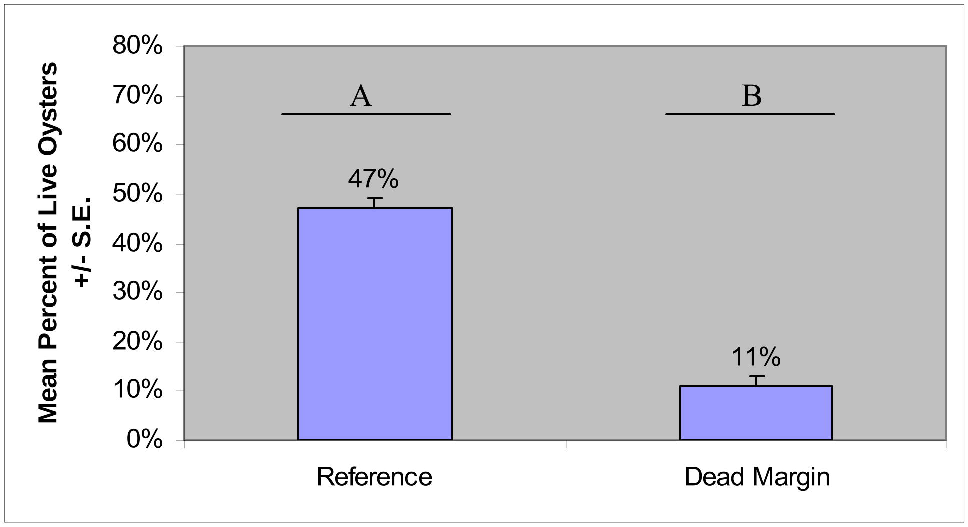

Figure 19. Comparison of the mean percent of live oysters (± S.E.) found on reference reefs and those affected by dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* results.

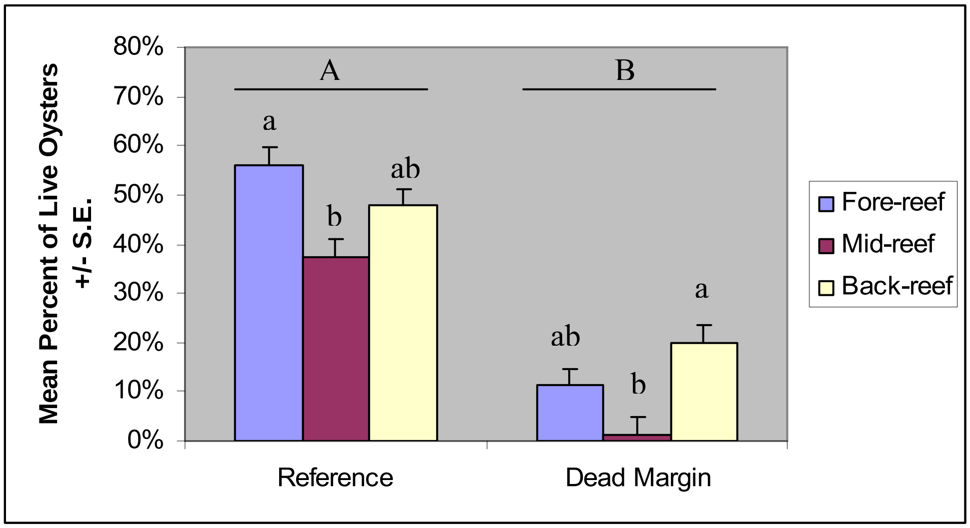

Figure 20. Comparison of the mean percent of live oysters (± S.E.) on three reef areas (i.e. fore-reef, mid-reef, and back-reef) of reference reefs and reefs containing dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the p ≤ 0.5 level according to Tukey *post hoc* comparisons. Lower-case letters refer to Tukey *post hoc* comparisons between the reef areas of reference reefs and reefs with dead margins (analyzed separately).

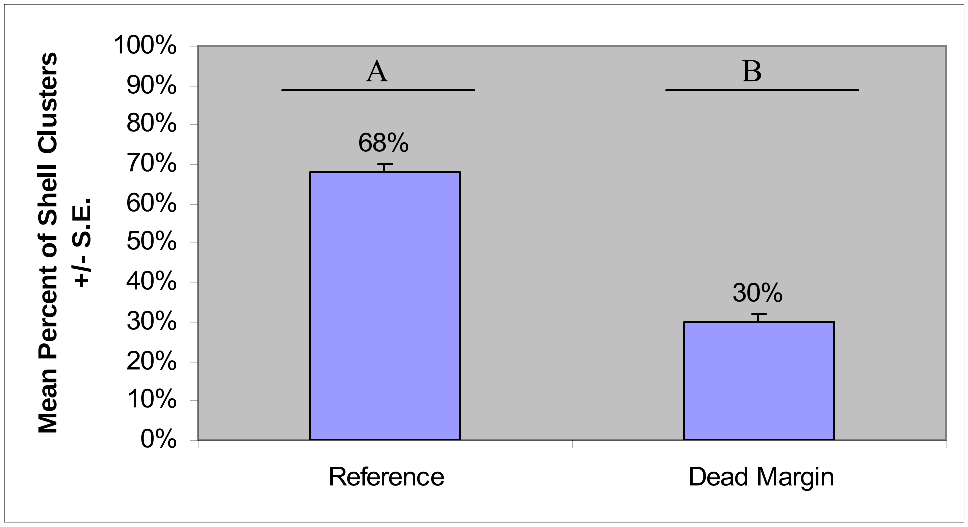

Figure 21. Comparison of the mean percent of oyster shell clusters (± S.E.) found on both reference reefs and those affected by dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* results.

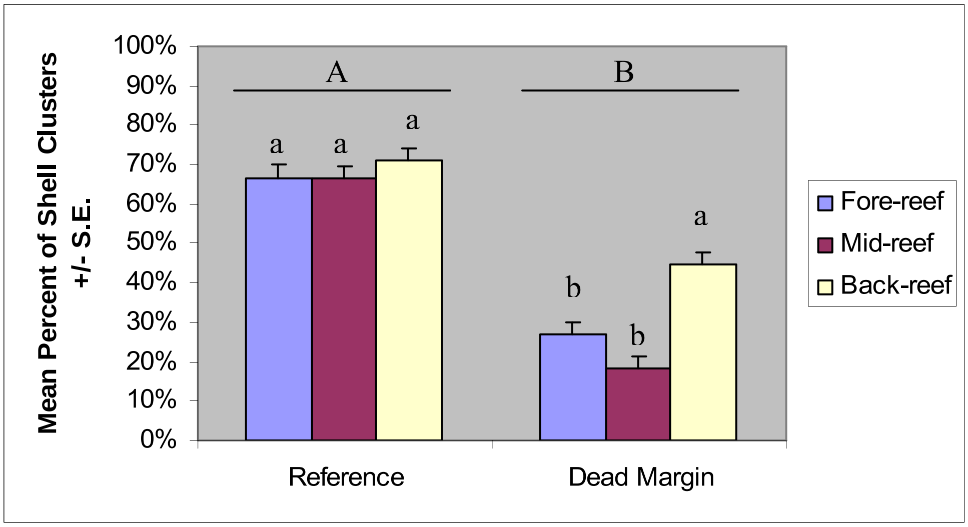

Figure 22. Comparison of the mean percent of shell clusters (± S.E.) on three reef areas (i.e. fore-reef, mid-reef, and back-reef) of reference reefs and those containing dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* comparisons. Lower-case letters refer to Tukey *post hoc* comparisons between the reef areas of reference reefs and reefs with dead margins (analyzed separately).

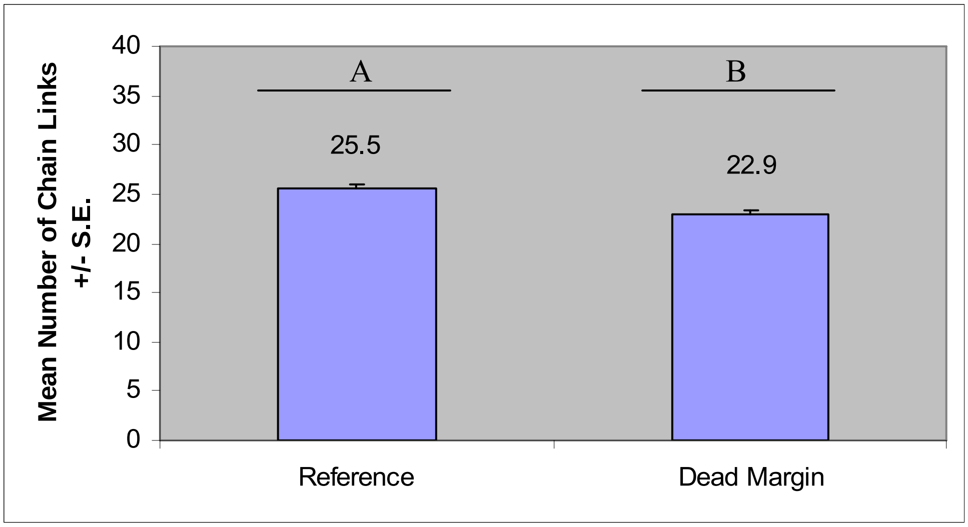

Figure 23. Comparison of the reef topography, measured by the mean number of chain links (± S.E.) across a 0.25 m^2 quadrat, of reference reefs and those affected by dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* results.

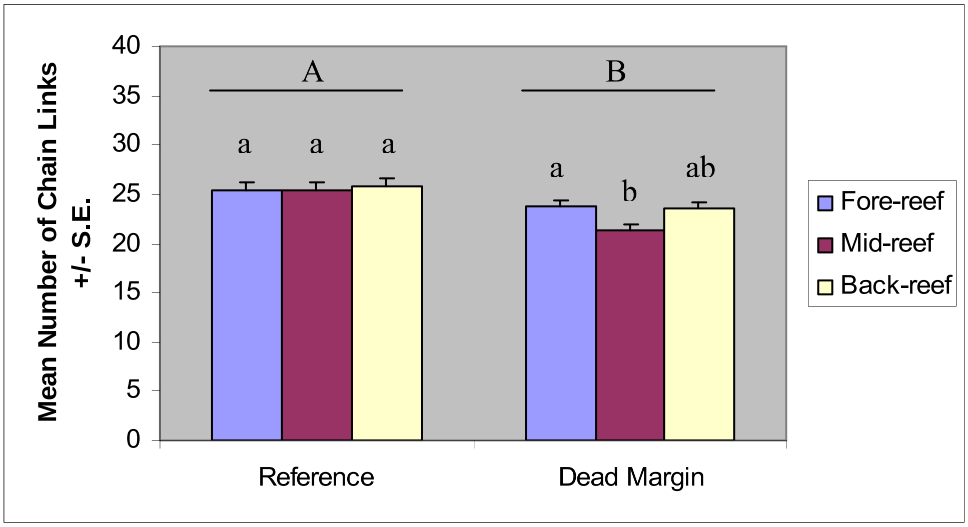

Figure 24. Comparison of the reef topography, measured by the mean number of chain links (± S.E.) across a 0.25 m^2 quadrat, on three reef areas (i.e. fore-reef, mid-reef, and back-reef) of both reference reefs and those affected by dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* results. There were no significant differences between reef areas of either reef type.

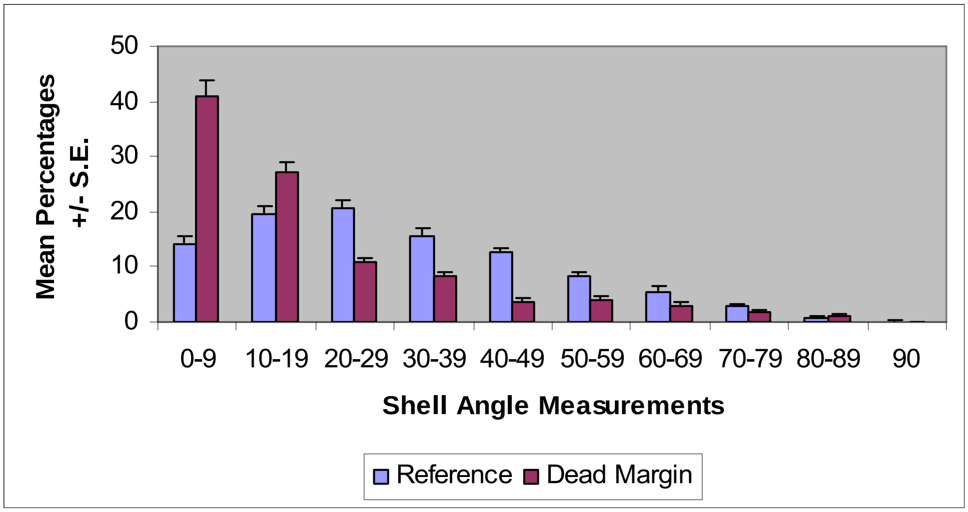

Figure 25. Distribution of the mean percentages of shell angles (± S.E.) collected on both reefs in reference condition and those containing dead margins.

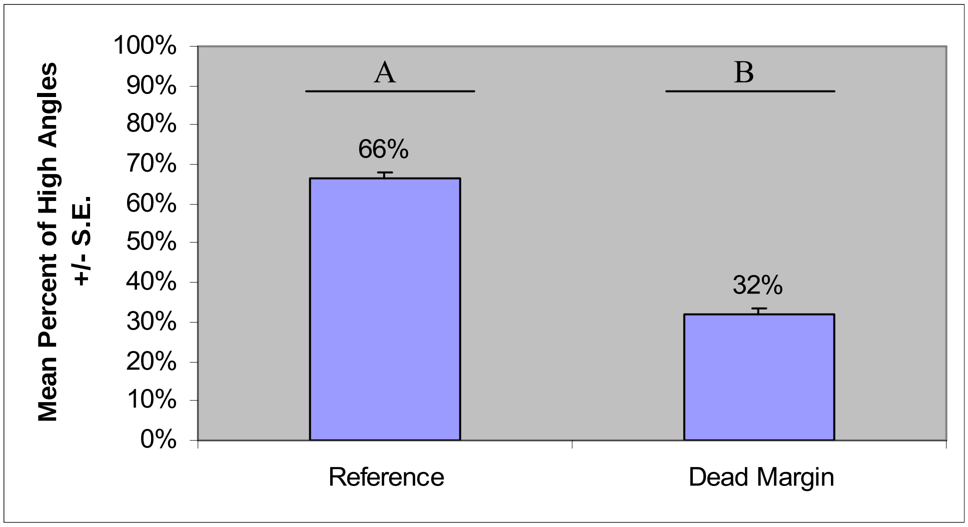

Figure 26. Comparison of the mean percent of shell angles ≥ 20° (± S.E.) found on both reference reefs and those affected by dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* results.

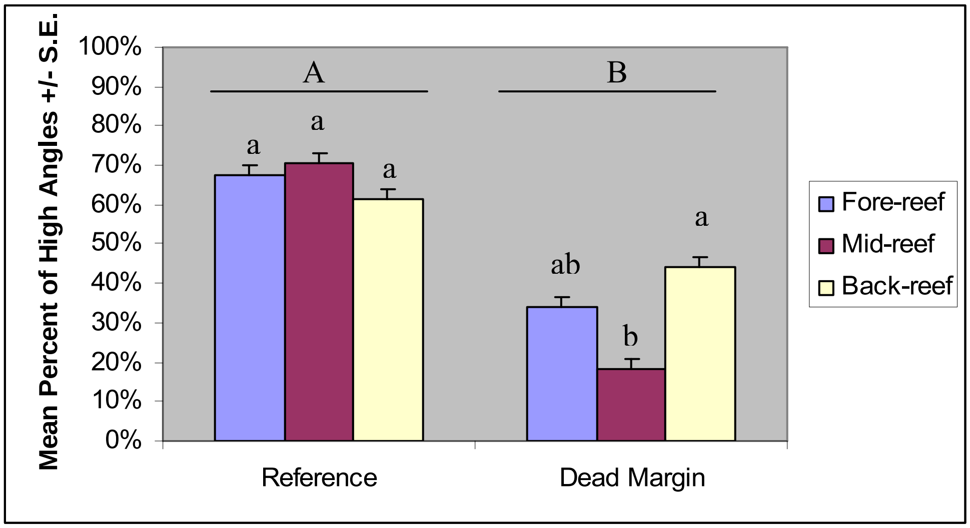

Figure 27. Comparison of the mean percent of shell angles ≥ 20° (± S.E.) on three reef areas (i.e. fore-reef, mid-reef, and back-reef) of reference reefs and those affected by dead margins.

Capital letters refer to the differences between reef type (reference and dead margin) at the $p \leq 0.5$ level according to Tukey *post hoc* comparisons. Lower-case letters refer to Tukey *post hoc* comparisons between the reef areas of reference reefs and reefs with dead margins (analyzed separately).

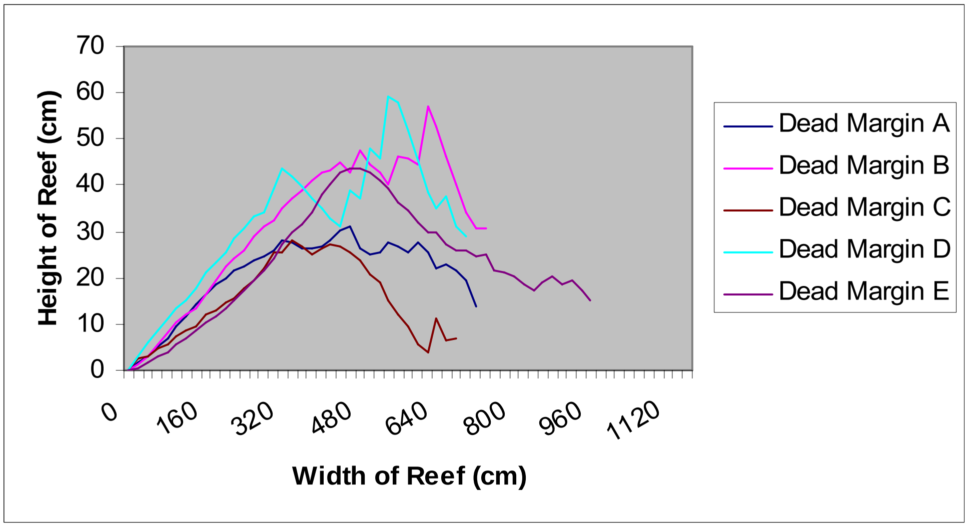

Figure 28. Vertical reef profiles of 5 reefs containing dead margins.

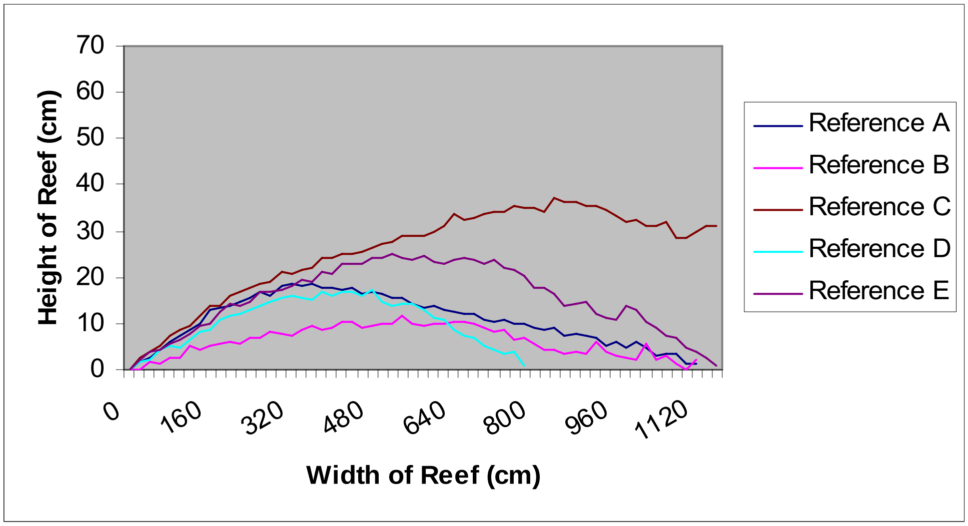

Figure 29. Vertical reef profiles of 5 reefs in reference condition.

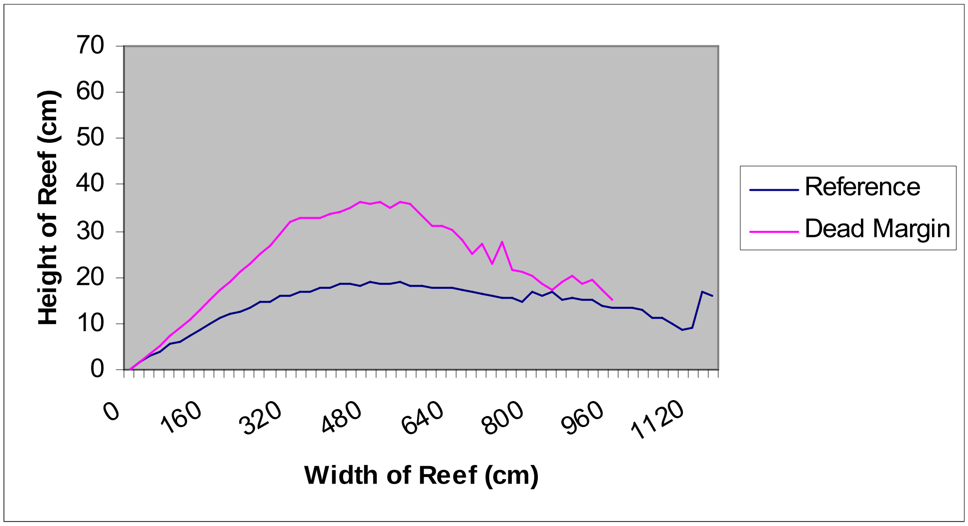

Figure 30. Mean overall shapes of the vertical profiles of reefs in reference condition and those affected by dead margins.

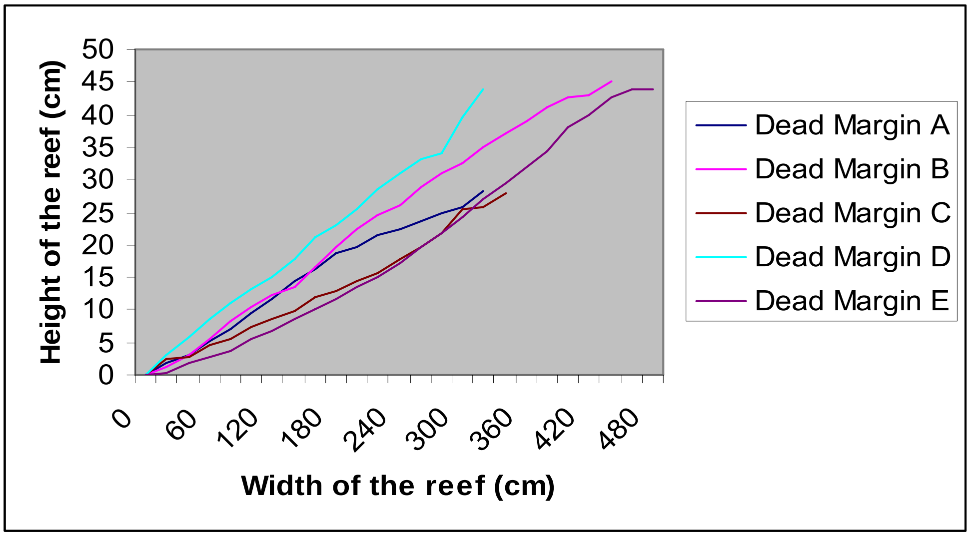

Figure 31. Profiles of the fore-reef area of 5 reefs affected by dead margins.

The slopes are as follows: A = 1.7981, B = 2.1587, C = 1.6103, D = 2.5664, and E = 2.0028.

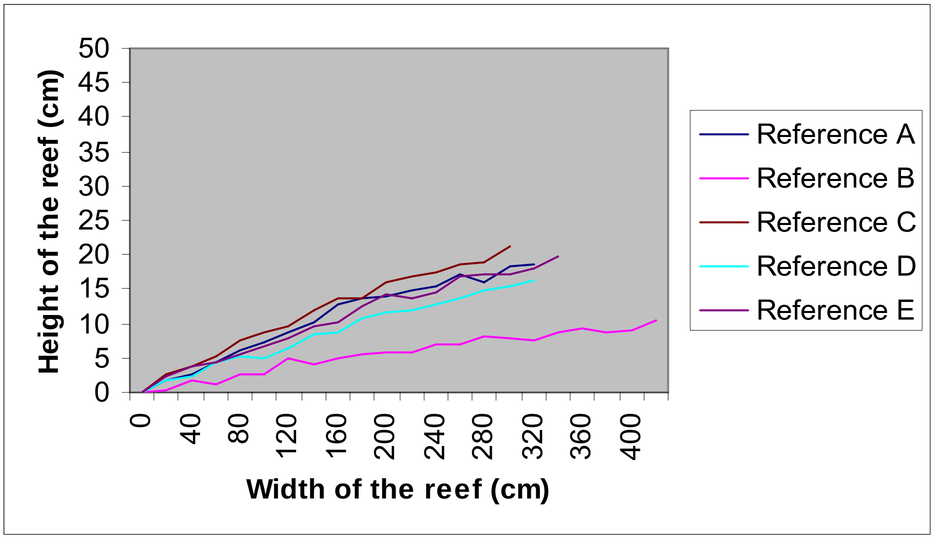

Figure 32. Profiles of the fore-reef area of 5 reefs in reference condition.

The slopes are as follows: A = 1.177, B = 0.4686, C = 1.3554, D = 1.0127, and E = 1.1209.

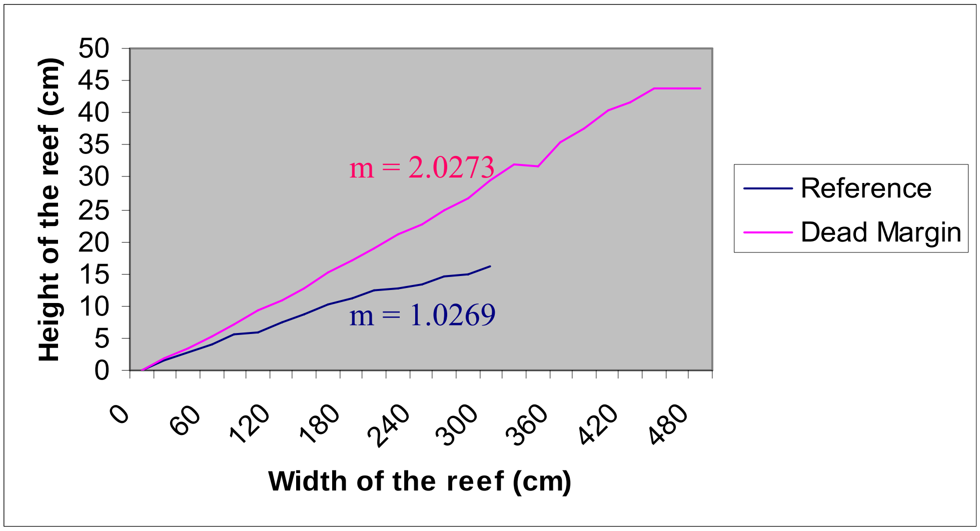

Figure 33. Mean slopes of the fore-reef area of reefs in reference condition and those affected by dead margins.

Figure 34. Experimental design for the manipulative enclosure experiment.

Two rows of enclosures were placed on the fore-reef area at each site (top picture); one row along the slope at the water's edge and one row on the flat, submerged portion. Within all enclosures, 12 oyster shells were oriented one of three ways (bottom pictures from left to right): (1) single and vertical, (2) single and horizontal, or (3) clustered.

Figure 35. Three predators used in the manipulative enclosure experiment.

From left to right: the blue crab *Callinectes sapidus* (~ 9 cm), the common mud crab *Panopeus herbstii* (~2 cm), and the Atlantic oyster drill *Urosalpinx cinerea* (~1.5 cm).

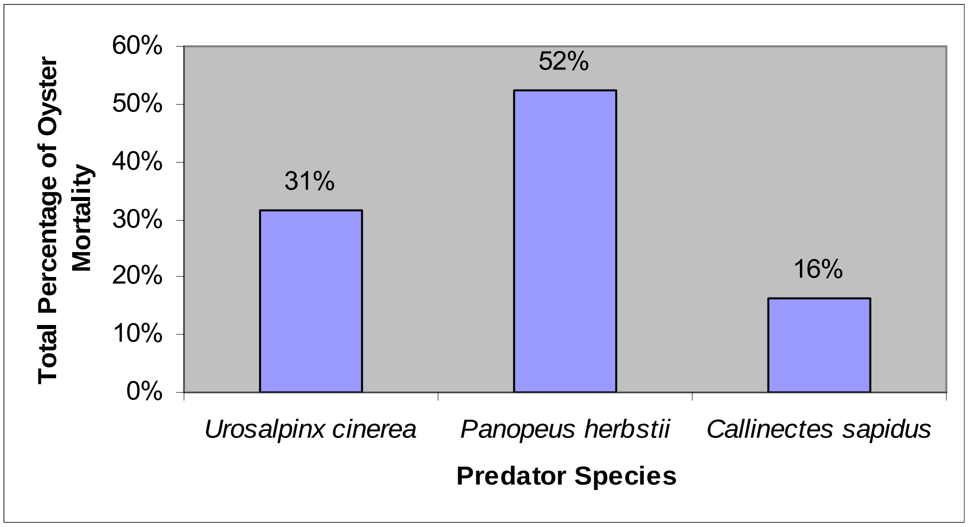

Figure 36. The total percentages of juvenile oyster mortality caused by three selected predators: the Atlantic oyster drill *Urosalpinx cinerea*, the common mud crab *Panopeus herbstii*, and the blue crab *Callinectes sapidus*.

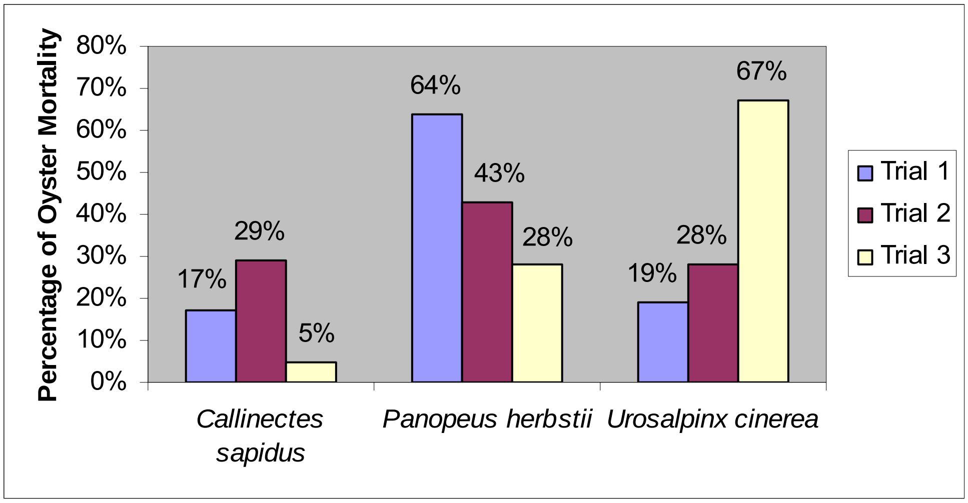

Figure 37. The percentages of oyster mortality caused by each predator species during all three trials.

APPENDIX B – TABLES

Table 1. Lift net deployment and retrieval dates.

Deployment	Retrieval
June 13, 2004	July 13, 2004
July 13, 2004	August 4, 2004
August 4, 2004	September 1, 2004
October 1, 2004	November 6, 2004
November 6, 2004	December 12, 2004
December 12, 2004	January 8, 2005
January 8, 2005	February 5, 2005
February 5, 2005	March 5, 2005
March 5, 2005	April 2, 2005
April 2, 2005	April 30, 2005
April 30, 2005	May 28, 2005
May 28, 2005	June 25, 2005

Table 2. Fifty-one mobile species collected in lift nets on oyster reefs within Mosquito Lagoon, Florida. The mean lengths and weights, including ranges, were calculated for each species.

						Date of Collection											
Phylum	**Species**	**Common Name**	**Total**	**Mean Length (cm)**	**Mean Weight (g)**	**6/04**	**7/04**	**8/04**	**10/04**	**11/04**	**12/04**	**1/05**	**2/05**	**3/05**	**4/05**	**5/05**	**6/05**
Echino-dermata	*Axiognathus squamatus*	Brooding brittle star	**1**	0.3±0.0	0.1±0.0											1	
	Ophionereis reticulata	Reticulated brittle star	**3**	0.2±0.1 (0.1-0.3)	0.1±0.0				1	1				1			
Annelida	*Phyllodoce fragilis*	Green oyster worm	**3**	0.5±0.1 (0.4-0.6)	0.1±0.0				1	2							
Mollusca	*Boonea impressa*	Oyster mosquito	**1**	0.3±0.0	0.1±0.0				1								
	Cerithiopsis emersoni	Awl miniature cerith	**26**	1.2±0.1 (1.0-1.6)	0.2±0.1 (0.1-0.6)	3	3		7	1	5		2	1	2	2	
	Cerithiopsis greeni	Green's miniature cerith	**1**	0.4±0.0	0.1±0.0									1			
	Cerithium atratum	Florida cerith	**5**	2.2±0.1 (2.1-2.4)	0.8±0.1 (0.7-1.0)												5
	Doriopsilla pharpa	Lemon drop sea slug	**18**	1.2±0.4 (0.7-2.0)	0.1±0.0				2			2		7	3	2	2
	Eupleura caudata	Thick-lipped drill	**2**	2.1±0.4 (1.7-2.5)	0.8±0.5 (0.3-1.3)				1				1				1
	Littorina irrorata	Marsh periwinkle	**2**	0.8±0.0 (0.8-0.9)	0.3±0.1 (0.2-0.3)						2						
	Nassarius vibex	Mottled dog whelk	**78**	1.1±0.0 (1.0-1.3)	0.4±0.0 (0.3-0.5)	2	4	12	11	5	10	8	1	8	5	8	4

	Pyrgo-cythara plicosa	Plicate mangelia	**48**	0.5±0.1 (0.5-0.8)	0.1±0.0 (0.1-0.2)	4	4		6		6	6	4	13	4		1
	Terebra salleana	Salle’s auger snail	**1**	0.35±0.00	0.1±0.0							1					
	Thais haemastoma floridana	Florida rock snail	**2**	0.8±0.1 (0.7-0.8)	0.2±0.1 (0.1-0.3)				2								
	Urosalpinx cinerea	Atlantic oyster drill	**19**	1.5±0.2 (1.2-1.9)	0.4±0.2 (0.2-0.9)	1	3	2	3	2	2		1	3	2		
Arthro-poda	*Alpheus hetero-chaelis*	Bigclaw snapping shrimp	**2489**	2.0±0.3 (1.6-2.5)	0.4±0.1 (0.3-0.5)	54	79	98	180	299	370	278	210	302	247	214	158
	Callinectes sapidus	Blue crab	**75**	3.0±0.4 (2.3-4.3)	3.4±0.8 (1.5-6.6)	2			9	30	9	11	4	6	3	1	
	Clibanarius vittatus	Striped hermit crab	**2**	5.0±0.1 (4.0-5.0)	2.5±0.1 (2.0-3.0)										1	1	
	Eury-panopeus depressus	Flat mud crab	**1217**	1.1±0.1 (0.8-1.3)	0.6±0.1 (0.5-0.8)	461	257	100	71	78	112	45	14	34	19	11	15
	Eurytium limosum	Broad-backed mud crab	**4**	1.0±0.0 (1.0-1.1)	0.3±0.1 (0.2-0.4)				1	1				1		1	
	Hetero-crypta granulate	Pentagon crab	**1**	1.5±0.0	0.5±0.0											1	
	Libnia dubia	Doubtful spider crab	**2**	3.8±0.3 (3.5-4.0)	24.3±0.3 (23.5-25)											1	1
	Menippe mercenaria	Stone crab	**3**	1.6±0.6 (1.0-2.1)	2.5±0.8 (1.7-3.3)		1			1					2		
	Palae-monetes vulgaris	Grass shrimp	**610**	2.9±0.2 (2.5-3.8)	0.4±0.1 (0.3-0.6)	1		2	14	28	261	52	92	66	18	44	32
	Panopeus herbstii	Atlantic mud crab	**534**	1.8±0.1 (1.4-2.1)	3.3±0.3 (1.5-4.3)	70	72	51	24	28	59	47	21	48	38	33	43

	Penaeus duorarum	Pink shrimp	**145**	4.6±0.5 (2.8-6.5)	1.3±0.3 (0.3-2.4)		3	9	5	3	6	5			40	56	18
	Petrolisthes armatus	Green porcelain crab	**584**	0.7±0.0 (0.6-0.8)	0.5±0.0 (0.3-0.6)	383	54	29	9	15	36	16	6	14	9	4	9
	Rhithro-panopeus harrisii	Harris's mud crab	**243**	0.9±0.1 (0.5-1.4)	0.6±0.1 (0.2-1.0)		6	17	26	17	46	11	12	50	15	13	30
	Squilla empusa	Common mantis shrimp	**1**	10.0±0.0	18.0±0.0												1
Chordata	*Archosargus probate-cephalus*	Sheepshead	**21**	7.2±0.9 (4.4-9.7)	12.7±1.9 (8.5-19.8)	3	1	1	7			4				3	2
	Bairdiella chrysoura	Silver perch	**7**	4.6±0.2 (4.0-5.0)	1.5±0.2 (1.0-2.0)	3			3								1
	Bathygobius soporator	Frillfin goby	**1**	4.0±0.0	0.8±0.0						1						
	Chasmodes saburrae	Florida blenny	**6**	4.3±0.3 (4.0-4.8)	1.2±0.4 (0.6-1.8)				1	3	1						1
	Cyprinidon variegatus	Sheepshead minnow	**3**	5.5±0.7 (4.1-6.5)	3.1±1.1 (1.1-4.8)	1				1	1						
	Diapterus auratus	Irish pompano	**1**	7.3±0.0	10.9±0.0			1									
	Floridich-thys carpio	Goldspotted killifish	**1**	6.8±0.0	7.8±0.0		1										
	Fundulus grandis	Gulf killifish	**2**	8.8±1.7 (7.1-10.5)	11.1±6.9 (4.2-17.9)					1			1				
	Gobionellus boleosoma	Darter goby	**54**	3.5±0.4 (2.2-5.0)	0.5±0.2 (0.2-1.2)			1	18	19	3	3		1	2		7
	Gobiosoma bosc	Naked goby	**736**	3.1±0.2 (2.6-3.8)	0.6±0.1 (0.3-1.0)	13	23	24	31	165	228	62	47	54	28	32	29
	Gobiosoma robustum	Code goby	**267**	2.9±0.3 (2.3-4.5)	0.5±0.2 (0.1-1.5)	1	3	12	49	139	27	6	3	4	12	3	8
	Haemulon flavo-	French grunt	**34**	3.7±0.3 (2.1-5.5)	1.1±0.2 (0.1-3.0)										6	25	3

	lineatum																
	Lagodon rhomboides	Pinfish	**148**	3.8±0.7 (2.3-7.7)	1.8±1.1 (0.1-8.3)	3	1	2		1		34	19	20	29	20	19
	Lucania parva	Rainwater killifish	**84**	2.5±0.3 (2.0-3.3)	0.3±0.1 (0.1-0.5)					5	1	11		5	4	47	11
	Lutjanus griseus	Gray snapper	**25**	5.9±1.1 (3.0-11.2)	6.5±3.0 (0.6-21.3)	1		1	1	10	2	4		2	1	3	
	Mugil cephalus	Striped mullet	**2**	22.0±1.0 (21-23)	13.4±0.6 (12.8-14)			1			1						
	Mugil curema	White mullet	**1**	11.5±0.0	16.0±0.0						1						
	Opsanus tau	Oyster toadfish	**40**	6.9±1.2 (2.3-9.0)	7.8±2.3 (0.2-13.3)	4	1	5		5		1		3	5	8	8
	Paralichthys albigutta	Gulf flounder	**1**	4.9±0.0	1.1±0.0										1		
	Paralichthys lethostigma	Southern flounder	**1**	3.6±0.0	0.4±0.0									1			
	Poecilia latipinna	Sailfin Molly	**109**	4.8±0.4 (4.3-5.6)	2.1±0.4 (1.6-3.0)	1		2		75	23	6	2				
	Sygnathus scovelli	Gulf pipefish	**16**	6.6±0.4 (5.6-8.6)	0.2±0.1 (0.1-0.4)											3	13

Table 3. Fourteen additional mobile species observed on oyster reefs in Mosquito Lagoon that were not collected within lift nets.

Phylum	Species Name	Common Name
Mollusca	*Aplysia brasiliana*	Sooty Sea Hare
	Busycon contrarium	Lightening Whelk
	Busycon spiratum	Pear Whelk
	Fasciolaria hunteria	Banded Tulip
	Fasciolaria tulipa	True Tulip
	Melongena corona	Crown Conch
	Pleuroploca gigantean	Florida Horse Conch
	Polinices duplicatus	Atlantic Moon Snail
Arthropoda	*Hexapanopeus angustifrons*	Narrow Mud Crab
	Limulus polyphemus	Horseshoe Crab
	Neopanope sayi	Say's Mud Crab
	Pinnotheres ostreum	Oyster Pea Crab
Chordata	*Symphurus plagiusa*	Blackcheek Tonguefish
	Arenaria interpres	Ruddy Turnstone

Table 4. A 3 factor nested ANOVA comparing species richness in lift nets.

The factors were reef type (fixed), site nested within reef type (random), and month (fixed).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	0.003	0.000	0.985	Site (Reef type)
Site (Reef type)	4	8.019	1.574	0.181	Residual
Month	11	37.699	9.340	< **0.001**	Residual
Residual	343	5.093			

Table 5. A 3 factor nested ANOVA comparing diversity in lift nets.
The factors were reef type (fixed), site was nested within reef type (random), and month (fixed).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	0.106	0.163	0.707	Site (Reef type)
Site (Reef type)	4	0.653	2.717	**0.030**	Residual
Month	11	2.832	17.414	< **0.001**	Residual
Residual	343	0.240			

Table 6. A 3 factor nested ANOVA comparing density in lift nets.

The factors were reef type (fixed), site was nested within reef type (random), and month (fixed).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	356.011	0.281	0.624	Site (Reef type)
Site (Reef type)	4	1267.778	4.430	**0.002**	Residual
Month	11	2379.484	10.278	< **0.001**	Residual
Residual	343	286.191			

Table 7. A 3 factor nested ANOVA comparing biomass in lift nets.

The factors were reef type (fixed), site was nested within reef type (random), and month (fixed).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	3.403	0.006	0.940	Site (Reef type)
Site (Reef type)	4	535.651	1.436	0.222	Residual
Month	11	2058.961	6.424	< **0.001**	Residual
Residual	343	373.010			

Table 8. A 3 factor nested ANOVA comparing total sediment loads collected per month at lift net sites.

The factors were reef type (fixed), site nested within reef type (random), and month (fixed).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	317305.223	1.961	0.234	Site (Reef type)
Site (Reef type)	4	161861.650	3.357	0.011	Residual
Month	11	124938.063	2.624	**0.004**	Residual
Residual	199				

Table 9. A 3 factor nested ANOVA comparing silt/clay fractions collected per month at lift net sites.

The factors were reef type (fixed), site nested within reef type (random), and month (fixed).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	39.068	0.687	0.454	Site (Reef type)
Site (Reef type)	4	56.862	0.871	0.482	Residual
Month	11	409.454	9.004	< **0.001**	Residual
Total	199	65.301			

Table 10. Mini lift net deployment and retrieval dates.

Deployment	Retrieval
June 22, 2005	June 29, 2005
June 29, 2005	July 6, 2005
July 6, 2005	July 13, 2005
July 13, 2005	July 20, 2005
July 20, 2005	July 27, 2005

Table 11. A 3 factor nested ANOVA comparing species richness found on three reef areas of both reference reefs and reefs affected by dead margins.

The factors were reef type (fixed), site nested within reef type (random), and reef area nested within site (fixed).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	130.904	21.885	**0.009**	Site (Reef type)
Site (Reef type)	4	5.981	0.223	0.920	Area(Site(Reef type))
Area (Site (Reef type))	12	26.767	16.774	< **0.001**	Residual
Residual	252	1.596			

Table 12. A 3 factor nested ANOVA comparing density found on three reef areas of both reference reefs and reefs affected by dead margins.

The factors were reef type (fixed), site nested within reef type (random), and reef area nested within site (fixed).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	1088.015	20.268	**0.011**	Site (Reef type)
Site (Reef type)	4	53.681	0.351	0.838	Area(Site(Reef type))
Area (Site (Reef type))	12	152.970	14.436	< **0.001**	Residual
Residual	252	10.596			

Table 13. A 3 factor nested ANOVA comparing biomass found on three reef areas of both reference reefs and those affected by dead margins.

The factors were reef type (fixed), site nested within reef type (random), and reef area nested within site (fixed).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	1340.900	30.622	**0.005**	Site (Reef type)
Site (Reef type)	4	43.789	0.289	0.879	Area(Site(Reef type))
Area (Site (Reef type))	12	151.440	6.515	< **0.001**	Residual
Residual	252	23.245			

Table 14. The distribution of 27 species found on three reef areas during mini lift net collection. Within each cell is the number of individuals collected over the five-week period.

		Reference Reefs			Reefs with Dead Margins		
Phylum	Species	Fore-reef	Mid-reef	Back-reef	Fore-reef	Mid-reef	Back-reef
Mollusca	*Cerithiopsis emersoni*			2	3		1
	Eupleura caudata				1		
	Nassarius vibex		1	1			8
	Pyrgocythara plicosa			2			2
	Thais haemastoma floridana			1			
	Urosalpinx cinerea	3		3	1		1
Arthropoda	*Alpheus heterochaelis*	40		29	6		23
	Callinectes sapidus		1		1		2
	Clibanarius vittatus				6		1
	Eurypanopeus depressus	77	38	33	10		20
	Menippe mercenaria		3	1			
	Palaemonetes vulgaris	1			2		42
	Panopeus herbstii	42	34	36	31		36
	Petrolisthes armatus	103	113	163	73		64
	Rhithropanopeus harrisii	2					2
Chordata	*Archosargus probatocephalus*	2		1			1
	Bathygobius soporator		1		1		
	Chasmodes	1					

	saburrae						
	Fundulus grandis	2					
	Gobionellus boleosoma	15		2	3		3
	Gobiosoma bosc	47		9	5		9
	Gobiosoma robustum	6		3	1		8
	Lagodon rhomboides		1	1			
	Lucania parva	1					14
	Lutjanus griseus	1			1		1
	Opsanus tau	1		1			
	Poecilia latipinna	4					

Table 15. A 3 factor nested ANOVA comparing the percent of live oysters found on reefs in reference condition and those affected by dead margins.

The factors were reef type (reference or dead margin), site, and area of reef (fore-reef, mid-reef, or back-reef).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	49262.241	42.800	< **0.001**	Site (Reef type)
Site (Reef type)	8	1150.991	0.785	0.621	Area(Site(Reef type)
Area (Site (Reef type))	20	1466.519	11.355	< **0.001**	Residuals
Residual	120	129.157			

Table 16. A 3 factor nested ANOVA comparing the percent of clusters found on reefs in reference condition and those affected by dead margins.

The factors were reef type (reference or dead margin), site, and area of reef (fore-reef, mid-reef, or back-reef).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	54657.852	54.497	< **0.001**	Site (Reef type)
Site (Reef type)	8	1002.944	1.059	0.428	Area(Site(Reef type)
Area (Site (Reef type))	20	947.204	4.970	< **0.001**	Residual
Residual	120	190.574			

Table 17. A 3 factor nested ANOVA comparing the topography, measured by number of chain links, of reefs in reference condition and those affected by dead margins.

The factors were reef type (reference or dead margin), site, and area of reef (fore-reef, mid-reef, or back-reef).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	272.027	6.157	**0.038**	Site (Reef type)
Site (Reef type)	8	44.180	1.813	0.134	Area(Site(Reef type)
Area (Site (Reef type))	20	24.367	2.814	< **0.001**	Residual
Residual	120	8.660			

Table 18. A 3 factor nested ANOVA comparing the percent of high angles (≥ 20º) of shells on reefs in reference condition and those affected by dead margins.

The factors were reef type (reference or dead margin), site, and reef area (fore-reef, mid-reef, or back-reef).

Factors	df	Mean Square	F	Significance	Denominator
Reef type	1	44355.634	13.825	**0.006**	Site (Reef type)
Site (Reef type)	8	3208.478	2.145	0.080	Area(Site(Reef type)
Area (Site (Reef type))	20	1495.528	8,117	< **0.001**	Residual
Residual	120	184.253			

Table 19. A one factor ANOVA comparing the widths of reference reefs and those affected by dead margins.

	Sum of Squares	df	Mean Square	F	Significance
Between groups	416160.0	1	416160.0	7.410	**0.026**
Within groups	449280.0	8	56160.0		
Total	865440.0	9			

Table 20. A one factor ANOVA comparing the heights of reference reefs and those affected by dead margins.

	Sum of Squares	df	Mean Square	F	Significance
Between groups	1256.081	1	1256.081	8.268	**0.021**
Within groups	1215.335	8	151.919		
Total	2471.435	9			

Table 21. A one factor ANOVA comparing the fore-reef area slopes of reference reefs and those containing dead margins.

	Sum of Squares	df	Mean Square	F	Significance
Between groups	2.502	1	2.502	20.296	**0.002**
Within groups	0.986	8	0.123		
Total	3.488	9			

Table 22. Contigency table combining mortality, species, and trial.

Trial	*Urosalpinx cinerea*	*Panopeus herbstii*	*Callinectes sapidus*
1	19.1%	64.3%	16.6%
2	27.8%	42.6%	29.6%
3	66.7%	28.0%	5.3%

Table 23. Pearson chi-square analysis of the contigency table combining mortality, species, and trial.

Trial	Value	df	Significance
1	72.708	2	**<0.001**
2	1.977	2	0.372
3	45.938	2	**<0.001**

Table 24. Analyses of log linear models involving mortality, species, and trial.

Model	df	Reference Model	df	Test Likelihood	df	Chi-square Threshold	Significant?
Mortality*Species 5422.4473	419	**All single** 5478.9879	421	56.5406	2	5.9915	Yes
Mortality*Trial 5337.5792	419	**All single** 5478.9879	421	141.4087	2	5.9915	Yes
Mortality*Species*Trial 396.6541	375	**All single, all double** 472.4643	379	75.8102	4	9.4877	Yes

REFERENCES

Arve, R. 1960. Preliminary report on attracting fish by oyster-shell plantings in Chincoteague Bay, MD. *Chesapeake Sci.* 1:58-65.

Bahr, L. M. 1976. Energetic aspects of intertidal oyster reef community at Sapelo Island, Georgia (USA). *Ecol.* 57:121.

__________ and W. P. Lanier. 1981. The Ecology of Intertidal Oyster Reefs of the South Atlantic Coast: A Community Profile. Fish and Wildlife Service, Office of Biological Services Report FWS/OBS-81/15. 105 pp.

Bartol, I. K., R. Mann, and M. Luckenbach. 1999. Growth and mortality of oyster (*Crassostrea virginica*) on constructed intertidal reefs. *J. Exp. Mar. Biol. Ecol.* 237:157-184.

Bell, S. S. and G. R. F. Hicks. 1991. Marine landscapes and faunal recruitment – a field test with seagrasses and copepods. *Mar. Ecol.-Prog. Ser.* 73(1):61-68.

_________, E.D. McCoy, and H. R. Mushinsky (eds.). 1991. Habitat structure: the physical arrangement of objects in space. Chapman & Hall, London, UK.

Bisker, R. and M. Castagna. 1987. Predation on single spat oysters *Crassostrea virginica* (Gmelin) by blue crabs *Callinectes sapidus* Rathbun and mud crabs *Panopeus herbstii* Milne-Edwards. *J. Shellfish Res.* 6:37-40.

Breitburg, D. L. 1992. Episodic hypoxia in Chesapeake Bay – interacting effects of recruitment, behavior, and physical disturbance. *Ecol. Monogr.* 62(4):525-546.

_____________. 1999. Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? *In*: M. W. Luckenbach, R. Mann, and J. A. Wesson (eds.), Oyster reef habitat restoration: a synopsis and synthesis of approaches. Virginia Institute of Marine Science Press, Gloucester Point, VA. pp. 239-250.

______________, L. D. Coen, M. W. Luckenbach, R. Mann, M. Posey, and J. A. Wesson. 2000. Oyster reef restoration: convergence of harvest and conservation strategies. *J. Shellfish Res.* 19(1):371-377.

Burrell, V. G., Jr. 1982. Overview of the South Atlantic oyster industry. *World Mariculture Soc. Spec. Publ.* 1:125-127.

Byers, J. E. 2002. Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. *Oecologia* 130(1):146-156.

Coen, L. D. and M. W. Luckenbach. 2000. Developing success criteria and goals for evaluating oyster reef restoration: Ecological function or resource exploitation? *Ecol. Eng.* 15(3-4):323-343.

__________, M. W. Luckenbach, and D. L. Breitburg. 1999. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. *Am. Fish. Soc. Sym.* 22:438-454.

___________, E. L. Wenner, D. M. Knott, B. W. Stender, N. H. Hadley, and N. Y. Bobo. 1996. Intertidal oyster reefs as critical estuarine environments: evaluating habitat use, development and function. *J. Shellfish Res.* 15:490.

Crabtree, R. E. and J. M. Dean. 1982. The structure of two South Carolina estuarine tide pool fish assemblages. *Estuaries* 5:2-9.

Dame, R. F. 1979. The abundance, diversity, and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. *Proc. Natl. Shell. Assoc.* 69:6-10.

__________. 1996. Ecology of Marine Bivalves: An Ecosystem Approach. CRC Press, Boca Raton, FL. 254 pp.

__________, R. G. Zingmark, and E. Haskin. 1984. Oyster reefs as processors of estuarine materials. *J. Exp. Mar. Biol. Ecol.* 83(3): 239-247.

Durako, M. J., M. D. Murphy, and K. D. Haddad. 1988. Assessment of Fisheries Habitat: Northeast Florida. *Fla. Mar. Res. Publ.* No. 45, 51 pp.

Eggleston, D. B. 1990. Behavioral mechanisms underlying variable functional responses of blue crabs, *Callinectes sapidus,* feeding on juvenile oysters, *Crassostrea virginica*. *J. Anim. Ecol.* 59(2):615-630.

_____________, W. E. Elis, L. L. Etherington, C. P. Dahlgren, and M. H. Posey. 1999. Organism responses to habitat fragmentation and diversity: Habitat colonization by estuarine macrofauna. *J. Exp. Mar. Biol.Ecol.* 236(1):107-132.

_____________, R. N. Lipcius, and A. H. Hines. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Mar. Ecol.-Prog. Ser.* 85(1-2):55-68.

Galtsoff, P. S. 1964. The American Oyster *Crassostrea virginica* (Gmelin). *Fish. Bull.* Vol. 64, 484 pp.

Gause, G. F. 1934. The struggle for existence. Williams & Williams, Baltimore, Maryland.

Glancy, T. P., T. K. Frazer, C. E. Cichra, and W. J. Lindberg. 2003. Comparative patterns of occupancy by decapod crustaceans in seagrass, oyster, and marsh-edge habitats in a Northeast Gulf of Mexico estuary. *Estuaries* 26(5):1291-1301.

Gosling, E. 2003. Bivalve Molluscs: Biology, Ecology, and Culture. Fishing News Books, MA.

Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85(4):995-1004.

Grant, J. and J. McDonald. 1979. Desiccation tolerance of *Eurypanopeus depressus* (Smith) (Decapoda, Xanthidae) and the exploitation of microhabitat. *Estuaries* 2(3):172-177.

________, C. T. Enright, and A. Griswold. 1990. Resuspension and growth of *Ostrea edulis*: a field experiment. *Mar. Biol.* 104:51-59.

Griffen, B. D. and J. E. Byers. 2006. Partitioning mechanisms of predator interference in habitats. *Oecologia* 146(4):608-614.

Grizzle, R. E. 1990. Distribution and abundance of *Crassostrea virginica* (Gmelin, 1791) (eastern oyster) and *Mercenaria* spp. (quahogs) in a coastal lagoon. *J. Shellfish Res.* 9:347-358.

_____________ and M. W. Castagna. 1995. Final report – oyster reef monitoring program in Canaveral National Seashore. 14 pp.

_____________, J. R. Adams, and L. J. Walters. 2002. Historical changes in intertidal oyster (*Crassostrea virginica*) reefs in a Florida lagoon potentially related to boating activities. *J. Shellfish Res.* 21(2): 749-756.

Harvey, K. 2004. 2003 Boating Accident Statistical Report. Florida Fish and Wildlife Conservation Commission, Division of Law Enforcement – Boating and Waterways Section. 68 pp.

Hines, A. H., A. M. Haddon, and L. A. Wiechert. 1990. Guild structure and foraging affect of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol.-Prog. Ser.* 67(2):105-126.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343-383.

Ingle, R. M. and C. E. Dawson Jr. 1952. Growth of the American oyster *Crassostrea virginica* (Gmelin) in Florida waters. *Bull. Mar. Sci. Gulf Caribb.* 2:393-404.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities – the role of biotic, abiotic, and spatial factors. *Can. J. Fish. Aquat. Sci.* 58(1):157-170.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.

Kennedy, V. S. 1991. Eastern Oyster. *In*: Funderburk, S. L., S. J. Jordan, J. A. Mihursky, and D. Riley (eds.), Habitat Requirements for Chesapeake Bay Living Resources. Chesapeake Research Consortium, Inc., Solomons, Maryland.

____________, R. I. E. Newell, and A. F. Elble (eds.). 1996. The Eastern Oyster, *Crassostrea virginica*. A Maryland Sea Grant Book, MD.

Knott, D. M. and R. A. King. 2006. *Petrolisthes armatus* - an introduced species in the South Atlantic Bight? Southeastern Regional Taxonomic Center. Website: http://www.dnr.sc.gov/marine/sertc/P%20armatus%20SOM.pdf

Leather, S. R. 1986. Insect species richness of the British Rosaceae: importance of host range, plant architecture, age of establishment, taxonomic isolation, and species-area relationship. *J. Anim. Ecol.* 55:841-860.

Lenihan, H. S. 1999. Physical-biological coupling on oyster reefs: How habitat structure influences individual performance. *Ecol. Monogr.* 69(3):251-275.

____________, and F. Micheli. 2001. Soft-sediment communities. Pp. 253-287. *In*: M. D. Bertness, S. D. Gaines, and M. E. Hay (eds.), Marine Community Ecology. Sinaeur Associates, Inc., Sunderland, MA.

_____________, and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances affects of hypoxia on oyster reefs. *Ecol. Appl.* 8(1):128-140.

Lipcius, R. N., and A. H. Hines. 1986. Variable Functional Responses of a Marine Predator in Dissimilar Homogeneous Microhabitats. *Ecology* 67(5):1361-1371.

Loosanoff, V. L. 1932. Observations on propagation of oysters in James and Corrotoman Rivers and the seaside of Virginia. Virginia Commission of Fisheries, p. 46.

_____________, and C. A. Nomejko. 1946. Feeding of oysters in relation to tidal stages and to periods of light and darkness. *Biol. Bull.* (Woods Hole) 90:244-264.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594-598.

Mackin, J. G. 1959. Mortalities of oysters. *Proc. Natl. Shell. Assoc.* 50:21-40.

McDonald, J. 1982. Divergent life history patterns in the co-occurring intertidal crabs *Panopeus herbstii* and *Eurypanopeus depressus* (Crustacea: Braychyra: Xanthidae). *Mar. Ecol.-Prog. Ser.* 8:173-180.

Menge, B. A. and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats – prey refuges in relation to consumer pressure-gradients. *Ecol. Monogr.* 51(4):429-450.

Meyer, D. L. 1994. Habitat partitioning between the Xanthid crabs *Panopeus herbstii* and *Eurypanopeus depressus* on intertidal oyster reefs (*Crassostrea virginica*) in southeastern North Carolina. *Estuaries* 17(3):674-679.

___________ and E.C. Townsend. 2000. Faunal utilization of created intertidal eastern oyster (*Crassostrea virginica*) reefs in the southeastern United States. *Estuaries* 23(1):34-45.

Micheli, F. 1997. Effects of predator foraging behavior on patterns of prey mortality in marine soft bottoms. *Ecol. Monogr.* 67(2):203-224.

___________ and C. H. Peterson. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conserv. Biol.* 13(4):869-881.

Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and pattern in plants and insects. *Ecology* 53:819-829.

Nelson, K. A., L. A. Leonard, M. H. Posey, T. D. Alphin, and M. A. Mallin. 2004. Using transplanted oyster (*Crassostrea virginica*) beds to improve water quality in small tidal creeks: a pilot study. *J. Exp. Mar. Biol. Ecol.* 298(2):347-368.

Newell, R. L. 1988. Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster? Chesapeake Bay Research Consortium, Baltimore, MD. 129:536-546.

Nichy, F. E. and R. W. Menzel. 1967. Mortality of intertidal and subtidal oysters in Alligator Harbor, Florida. *Proc. Natl. Shellfish. Assoc.* 52:33-41.

NOAA. 2005. National Climatic Data Center: 2005 LCD Annual Summary with Comparative Data for Daytona Beach, Florida. Website: http://www1.ncdc.noaa.gov/pub/orders/B29D3DA3-F3EA-62ED-1643-5536F2586C9F.PDF

NOAA. 2006. Applied Uses: Water Quality Indicators. Website: http://www.csc.noaa.gov/benthic/cdroms/sav_cd/html/images/irl.gif

Officer, C. B., T. J. Smayda, and R. Mann. 1982. Benthic filter feeding – a natural eutrophication control. *Mar. Ecol.-Prog. Ser.* 9(2):203-210.

Paine, R. T. 1969. A note on trophic complexity and community stability. *Am. Nat.* 103(929):91-93.

Posey, M. H., T. D. Alphin, C. M. Powell, and E. Townsend. 1999. Use of oyster reefs as habitat for epibenthic fish and decapods. pp. 133-159 *In*: M. W. Luckenbach, R. Mann, and J. A. Wesson (eds.), Oyster reef habitat restoration: a synopsis and synthesis of approaches. Virginia Institute of Marine Science Press, Gloucester Point, Virginia.

Provancha, J. A., C. R. Hall, and D. M. Oddy. 1992. Mosquito Lagoon Environmental Resources Inventory. NASA Technical Memorandum 107548. The Bionetics Corporation. Kennedy Space Center, Florida.

Purchon, R. D. 1977. The Biology of the Mollusca. Pergamon, Oxford, UK.

Roegner, G. C. and R. Mann. 1995. Early recruitment and growth of the American oyster *Crassostrea virginica* (Bivalvia, Ostreidae) with respect to tidal zonation and season. *Mar. Ecol.-Prog. Ser.* 117(1-3):91-101.

SeaWorld. 2002. Animal Information Database. Website: http://www.seaworld.org/wild-world/zoo-research/indian-river-project/images/irlmap.gif

Seitz, R. D., R. N. Lipcius, A. H. Hines, and D. B. Eggleston. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology* 82(9):2435-2451.

Seliger, H. H., J. A. Boggs, and W. H. Biggley. 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. *Science* 228(4695):70-73.

Sellers, M. A. and J. G. Stanley. 1984. Species profile: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) – American oyster. U.S. Fish and Wildl. Serv. FWS/OBS-82/11.23. U.S. Army Corps of Engineers, TR EL-82-4. 15 pp.

Smithsonian Institution. 2001. Indian River Lagoon Species Inventory Report. Website: http://www.sms.si.edu/irlspec/index.htm

Summerson, H. C. and C. H. Peterson. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar. Ecol.-Prog. Ser.* 15(1-2):63-77.

Tolley, S. G., A. K. Volety, and M. Savarese. 2005. Influence of salinity on the habitat use of oyster reefs in three southwest Florida estuaries. *J. Shellfish Res.* 24:127-138.

Tremain, D. M. and D. H. Adams. 1995. Seasonal variations in species diversity, abundance, and composition of fish communities in the northern Indian River Lagoon, Florida. *Bull. Mar. Sci.* 57(1): 171-192.

USDOC (U.S. Department of Commerce). 1997. Magnuson-Stevens Fishery Conservation and Management Act, as amended through October 11, 1996. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/SPO-23. U.S. Government Printing Office, Washington, D.C.

Wall, L. M., L. J. Walters, R. E. Grizzle, and P. E. Sacks. 2005. Recreational boating activity and its affect on the recruitment and survival of the oyster *Crassostrea virginica* on intertidal reefs in Mosquito Lagoon, Florida. *J. Shellfish Res.* 24:965-974.

Walters, L. J., A. Roman, J. Stiner, and D. Weeks. 2001. Water Resources Management Plan. Canaveral National Seashore, Florida.

Wells, H. W. 1961. The fauna of oyster reefs with special reference to the salinity factor. *Ecol. Monogr.* 60:449-469.

Wenner, E., H. R. Beatty, and L. Coen. 1996. A quantitative system for sampling nekton on intertidal oyster reefs. *J. Shellfish Res.* 15:769-775.

Wilson, W. H. 1990. Competition and predation in marine soft-sediment communities. *Annu. Rev. Ecol. Syst.* 21:221-241.

Woodley, C. M. and M. S. Peterson. 2003. Measuring responses to simulated predation threat using behavioral and physiological metrics: the role of aquatic vegetation. *Oecologia* 136(1):155-160.